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# THE BOTANICAL GAZETTE

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## JOHN MERLE COULTER

(WITH PORTRAIT)

JOHN MERLE COULTER, who founded the BOTANICAL GAZETTE, and who edited it for more than half a century, died December 23, 1928, at Yonkers, New York.

The Gazette in its infancy was a very unpretentious undertaking, consisting each month of a four-page leaflet, the first number of which was issued at Hanover, Indiana, in November, 1875. At first the new journal was known as the Botanical Bulletin, but from the second volume it has been known as the Botanical Gazette, the change of name being made out of regard for the previously existing Bulletin of the Torrey Botanical Club.

For the first few years M. S. COULTER, now better known as STANLEY COULTER, was coeditor with his brother. In 1883 CHARLES R. BARNES, then at Purdue University, and J. C. ARTHUR, then at Charles City, Iowa, became joint editors with Professor COULTER. At that time the journal was much enlarged, and was organized into departments. For many years the Gazette was published by the editors, who bore all financial, as well as editorial responsibility for the journal. At first the subscription price was but $1.00 a year, and for several years there was no advertising matter, yet almost from the outset the journal paid its way. In the first twenty years of publication the home of the Gazette changed with the abode of one of the editors; at first it was issued from Hanover, Indiana, then from Crawfordsville, Indiana, and Bloomington, Indiana, the suc-

cessive homes of Professor COULTER. From Bloomington it went to Madison, Wisconsin, at that time the residence of Professor BARNES.

In 1896 the Botanical Gazette was taken over by the University of Chicago Press, under whose auspices it has since been published. At the same time several prominent American botanists became associate editors, and the following year a group of foreign botanists was added to the list of associate editors. Commencing with 1900, Professor ARTHUR ceased to be a coeditor with COULTER and BARNES, and his name was added to the list of associate editors. Thenceforward the main editorial responsibility rested with Professor COULTER and Professor BARNES, with the assistance of the other members of the botany staff at the University of Chicago. Upon the death of Professor BARNES in 1910, Professor COULTER once more assumed the chief editorial responsibility, and he continued in this capacity until 1926, when the main responsibility passed to the writer of this sketch. Even after the chief editorial burden was set aside, Professor COULTER continued to maintain a lively interest in the journal, contributing many reviews and performing various other editorial functions.

The growth of the Botanical Gazette in size and in the number of fields covered in its articles is a measure of the growth of botany in America since 1875. At first the contributions were mostly short taxonomic or floristic notes, without illustrations. Gradually the major contributions lengthened, were more profound in character, and often were illustrated. Morphology was early added to taxonomy as a field of interest, and later contributions appeared in physiology, ecology, mycology, pathology, genetics, and the other fields of modern botany. If Professor COULTER had no other monument than the Botanical Gazette, his place in the botanical roll of honor would forever be assured.

JOHN MERLE COULTER was born in Ningpo, China, November 20, 1851, the son of missionary parents. Upon the death of his father in 1853, his mother returned to America with the children, taking up residence at Hanover, Indiana, her father's home. His boyhood days were spent in southern Indiana, mostly at Hanover. He attended Hanover College, from which he was graduated in 1870 with the degree of Bachelor of Arts. His first teaching position was at a

Presbyterian Academy at Logansport, Indiana, where he remained from the autumn of 1870 through the spring of 1872, not as a teacher of botany, but as a teacher of Latin.

In 1872 an event occurred which had a profound influence on Professor COULTER'S subsequent career. He was given an opportunity to join the famous Hayden Survey of the Yellowstone, which occupied most of his attention for two years. His appointment was as assistant geologist, but while spending some weeks at Ogden, Utah, where the party was outfitting, he spent his time in collecting and studying the plants of the neighborhood. This came to the notice of Dr. HAYDEN, who needed a botanist, since the originally appointed botanist of the expedition had failed him. So the position was given to Mr. COULTER, who always regarded this incident as a veritable turning point in his life.

The degree of Master of Arts was conferred on the young botanist in 1873 by Hanover College, and from 1874 to 1879 he was Professor of Natural Sciences at that institution. It was during these years that he and his brother founded the Botanical Gazette. In 1879 he was called to the chair of Biology at Wabash College, where he remained until 1891. In 1882 he received the degree of Doctor of Philosophy at the University of Indiana, which called him to the botanical professorship and the presidency in 1891. In 1893 he went to the presidency of Lake Forest University. In 1896 he was called to the headship of the new Department of Botany at the University of Chicago, where he remained until his retirement in 1925. In the latter year he took up his residence at Yonkers, New York, the seat of the Boyce Thompson Institute for Plant Research, which he helped to organize, and of whose Board of Directors he was a member from the outset.

Professor COULTER was a charter member of the Botanical Society of America, and was twice its president. He was a long-time member of the American Association for the Advancement of Science and its president in 1919, a member of the National Academy of Sciences, and a member of many other scientific societies at home and abroad.

The early work of Professor COULTER was mostly in the field of taxonomy. This was natural enough, for in the seventies and eighties most American botany was in this field. When he went to Washing-

ton to work up his western collections, he chanced to meet ASA GRAY, who took a great interest in the young Indiana botanist; from that time forth until the death of GRAY in 1888, the friendship between the two was close and intimate. COULTER always attributed much of his success to the influence of GRAY. The Hayden expedition naturally enough suggested the early attention of Mr. COULTER to the flora of the Rocky Mountains, and one of his earliest works was a synopsis of the flora of Colorado, published in 1874 in collaboration with T. C. PORTER. Commencing with 1875, Professor COULTER contributed many articles to the Botanical Gazette, the first of which were mainly taxonomic. In 1885 there appeared his well known Manual of the Botany of the Rocky Mountain Region, and in 1909 was issued the Manual of Rocky Mountain Botany in collaboration with AVEN NELSON. His Botany of Western Texas appeared as a contribution of the United States National Herbarium in 1891–1894.

In 1881 Professor COULTER issued, in collaboration with CHARLES R. BARNES, a Catalogue of the Phaenogamous and Vascular Cryptogamous Plants of Indiana. Alone or in collaboration Professor COULTER issued a number of taxonomic monographs, as his Revision of the North American Hypericaceae in 1886; Synopsis of the North American Pines (with J. N. ROSE) in 1886; various works on the Umbelliferae from 1887 to 1909, especially Revision of North American Umbelliferae in 1888, Synopsis of Mexican and Central American Umbelliferae in 1900, Monograph of North American Umbelliferae in 1900, and North American Umbelliferae in 1909, all four with J. N. ROSE. In 1894 and 1896 were published works on Cacti. In 1890 was issued the sixth edition of GRAY'S Manual of Botany, under the editorship of SERENO WATSON and JOHN M. COULTER.

Early in his career Professor COULTER turned part of his attention to the developing field of morphology, and many outstanding articles and books represent his contribution in this line of endeavor. Perhaps his first contribution in this field was a study of the development of a dandelion flower, published in 1883. Following this was a paper in 1887 on the development of the Umbellifer fruit. But it was after coming to Chicago that his great contributions to morphology were made, mostly in collaboration with CHARLES J. CHAM-

BERLAIN. The most noteworthy of these were the volumes on the Morphology of Spermatophytes, Morphology of Angiosperms, and Morphology of Gymnosperms, published respectively in 1901, 1903, and 1910. Other morphological contributions were issued in the form of papers on the Phylogeny of Angiosperms in 1903, the Embryogeny of *Zamia* (with C. J. CHAMBERLAIN) in 1903, Development of Morphological Conceptions in 1904, Gametophytes and Embryo of *Torreya taxifolia* (with W. J. G. LAND) in 1905, Relation of Megaspores to Embryo Sacs in Angiosperms in 1908, Embryo Sac and Embryo of *Gnetum gnemon* in 1908, Evolutionary Tendencies among Gymnosperms in 1909, An American *Lepidostrobus* (with W. J. G. LAND) in 1911, the Endosperm of Angiosperms in 1911, and the Origin of Monocotyledony (with W. J. G. LAND) in 1914.

In the field of botanical textbooks Professor COULTER made rich contribution. In 1886 appeared a Handbook of Plant Dissection by ARTHUR, BARNES, and COULTER, often familiarly called a botany ABC. Plant Relations appeared in 1901, Plant Structures in 1904, Plant Studies in 1904, Textbook of Botany in 1906, and Elementary Studies in Botany in 1913. Professor COULTER wrote the morphological section of the more advanced Textbook of Botany, issued in 1910 in collaboration with CHARLES R. BARNES and HENRY C. COWLES.

Professor COULTER contributed also to fields other than those just noted. In 1914 he issued a book on the Fundamentals of Plant Breeding, and a book on the Evolution of Sex in Plants; and in 1916 a book on Evolution, Heredity, and Eugenics. He published from time to time papers on evolution, on various educational and religious subjects, and on topics dealing with the relation between science and religion.

Great as were Professor COULTER'S contributions to taxonomy, morphology, and other fields, and as a botanical editor, it is probable that his greatest single influence was as a teacher. He was an inspiring lecturer, a splendid counselor, and a devoted friend. His kindly sympathy and help drew all his students closely to him, and made them devoted followers. He inspired many men and women to devote themselves to botanical research and botanical teaching.

This was true at Hanover, Crawfordsville, Bloomington, and Lake Forest, but it was particularly true at Chicago, for there as nowhere else in his previous experience came opportunity to teach, influence, and inspire graduate students from colleges and universities from this and other countries. During his headship at Chicago 175 students attained under him the degree of Doctor of Philosophy, and almost as many attained the degree of Master of Science. Shortly after coming to Chicago he initiated the series of researches known as "Contributions from the Hull Botanical Laboratory." These include contributions made by Professor COULTER and other members of the Chicago botany staff, nearly all of the Doctor's theses, and many of the Master's theses. Nearly 400 of these have been issued in the Botanical Gazette.

The students of Professor COULTER have more than once shown their appreciation of their leader. In 1916, at the occasion of the quarter centennial of the University of Chicago, the botany doctors, then 80 in number, presented to him a volume giving the record of the doctors to that date. On December 27, 1928, at New York, there culminated a movement to establish at Chicago a JOHN M. COULTER Research Fellowship in Botany. This movement had been initiated by the Chicago botany doctors two years previously at Philadelphia, and at New York it was announced that pledges amounting to more than $25,000 were in hand, thus assuring the fellowship. This fund was subscribed by 130 doctors and 75 masters and former students of Professor COULTER. It is expected that the first fellowship on this foundation will be available in the academic year 1929–1930. Almost simultaneously with the announcement of the COULTER Fellowship, there was presented to Mrs. COULTER a silver service and a volume of testimonials to Professor COULTER from the botanists of America. It had been the hope that Professor COULTER would be present in person to hear the announcement of the Fellowship and to receive the silver service and the volume of testimonials. It was a tragic coincidence that he died but a few days before these events were scheduled to take place. It is, however, a matter of satisfaction that before he died he was apprised of both events and was highly gratified because of them.

A scientific journal, such as the BOTANICAL GAZETTE, is hardly the place to speak more intimately and appreciatively of Professor COULTER'S life and influence, even though this is the journal that he founded and edited for so many years. It is perhaps enough to say that there has passed from us a man loved and admired, not only by his fellow botanists and former students, but also by many in other fields of science, and in every walk in life; that there has gone a great teacher, a gifted editor, an inspiring lecturer, and a facile writer; and that, as he himself said on the death of Professor BARNES, "a priceless asset has become a memory."—H. C. COWLES.

# MEIOSIS IN POLLEN MOTHER CELLS OF STRAINS OF OENOTHERA PRATINCOLA BARTLETT[1]

CHANDRAKANT G. KULKARNI

(WITH PLATES VII–IX)

## Introduction

Investigations of the nuclear behavior in the pollen development of *Oenothera lamarckiana* and certain of its derivatives, together with some of the other large-flowered, generally cross-pollinated species of *Oenothera*, have made clear some of the reasons for the peculiar genetical behavior that characterizes this genus, even though all the hypotheses proposed are in some respects at variance with one another. So far, few cytological investigations of the small-flowered, generally self-pollinated species have been made. There are papers by DAVIS (**23**), EMERSON (**32**), CLELAND (**18, 19**), and VALCANOVER (**88**); there are no cytological publications whatever on the types studied genetically by BARTLETT, FRIEDA COBB BLANCHARD, LARUE, KLAPHAAK, and MARAÑON at the University of Michigan. Of these, *O. pratincola* is the foremost in interest, due to the fact that it has been most intensively studied and has given rise to the most mutations. In addition to many genetical phenomena that are common with the large-flowered species, *O. pratincola* shows behavior peculiar to itself and to other small-flowered species (LARUE and BARTLETT **56, 57**).

The strains of *O. pratincola* used in this research are those whose history has been published by BARTLETT (**2, 3, 5**) and COBB and BARTLETT (**20**). Although the eight strains of this species from Lexington, Kentucky are morphologically alike, the strain designated E has a genetical behavior differing from the other seven. This strain gave rise to variants in such large numbers that BARTLETT (**4, 5**) designated the phenomenon mass mutation. Some of the mutations produced by the other strains are also produced by strain E, but the latter is peculiar in throwing a series of forms with narrow,

[1] Papers from the Department of Botany of the University of Michigan, no. 298. Walker prize essay of the Boston Society of Natural History, 1928.

strongly revolute, thick-veined leaves, which do not occur in the other strains. Mut. *formosa*, an example in this series, has been completely described and illustrated (BARTLETT 5). Mut. *formosa* was chosen for this study because, being the most fertile of the revolute-leaved forms, it was most successfully used in crosses of genetical and cytological significance for the problems under discussion.

*Oenothera pratincola* strain C gives rise to mutations of several kinds in every generation (BARTLETT 3). This strain differs from strain E in that it has never shown mass mutation since coming under cultivation. Strain C is typical of the seven others, and was chosen for crossing with strain E and also with mut. *formosa*.

Strain M comes from a cross between mut. *formosa* and strain C, the former being the female parent. It was designated "M" because it shows Mendelian segregation. When mut. *formosa* is pollinated by strain C, the $F_1$ plants are all f. *typica*, that is, similar to *O. pratincola*. The $F_2$ generation splits into 3 f. *typica:* 1 mut. *formosa* (COBB 21). This strain becomes of great cytological and genetical interest because simple cases of Mendelian inheritance in *Oenothera* are uncommon. The first described case of Mendelian inheritance is afforded by *O. brevistylis*, which acts in crosses as a recessive with *O. lamarckiana* and even with unrelated species (DE VRIES 73, DAVIS 25, 26). The *brevistylis* complex, when introduced into the form *nanella-brevistylis*, is also recessive; when this plant is crossed to *nanella* and to *lamarckiana* it segregates in the $F_2$ in proportions close to the 1:3 Mendelian ratio (DAVIS 27). Another example showing Mendelian behavior is the dwarf mutation from *O. gigas* which also acts as a recessive in crosses with its parent (DE VRIES 92). It has been the contention of GATES (44, 45) that *O. rubricalyx* acts as a Mendelian dominant in crosses with *O. rubrinervis*, but SHULL (77) offers another interpretation. Another character, "old-gold," a flower color which arose as a gene mutation from *O. lamarckiana*, has recently been added by SHULL (80) to the list. In crosses with its parent *O. lamarckiana*, which has yellow flowers, this character acts as a Mendelian recessive.

## Material and methods

The material on which this research is based was collected from pedigreed cultures in the Botanical Garden of the University of

Michigan, during the summers of 1925 and 1926. Various fixing fluids were used, of which only one (weak Flemming) failed entirely to give satisfactory results. One of Allen's modification of Bouin's solution (saturated aqueous solution of picric acid 75 cc., commercial formalin 25 cc., glacial acetic acid 5 cc., chromic acid 1 gm., and urea 2 gm.) gave excellent results. Allen's modification of Bouin's solution as used by CLELAND (**16**) was also very good. Strong Flemming with 1 per cent urea and 1 per cent maltose added, yielded very satisfactory fixations, as good as those of Allen's modification of Bouin's. Straight Bouin's solution also proved excellent. The fixations in chromo-acetic solution containing chromic acid 1 gm., glacial acetic acid 3 cc., and distilled water 200 cc. were generally good. When using strong Flemming it is necessary to wet and scrub the anthers quickly with a stiff hair brush, as suggested by DAVIS (**23, 24**), so as to loosen the waxy coat that envelops them, and thus facilitate quick penetration by the killing fluid. If this procedure is not followed with great patience and care, the fixations in strong Flemming are likely to be generally very poor.

Twelve fixations were made from four plants of *O. pratincola* strain E, six from three plants of *O. pratincola* mut. *formosa*, nine from three plants of *O. pratincola* strain C, and eight from four plants of *O. pratincola* strain M. Each fixation consisted of twenty-five buds.

Whenever a fixation was secured from a plant, pollen counts were made on four or five buds, picked at random, to determine the percentage of good pollen. The results of these tests are included in table I, and show for the four strains good pollen averaging about 86 per cent. Table I also gives the time at which fixations were made, the length of time the buds were left in the fixing fluid, the kind of fixing fluid used, and the results from various fixations.

When strong Flemming solution was used, the buds were left in the solution for two to three hours, and were then transferred for 24 hours to chromo-acetic solution, to avoid the excessive blackening of the material that ensues from the action of the osmic acid. In case of Bouin's solution and its modifications, three to six hours in the fluid gave excellent results.

All the stages of cell division were plentifully obtained in the

majority of fixations, made between 11:30 A.M. and 3:30 P.M. The material was dehydrated through grades of alcohol, cleared in xylol, and imbedded in paraffin. Longitudinal sections, varying from 6 to

TABLE I

QUALITY OF FIXATION AND TIME OF FIXING; POLLEN CONDITION OF PLANT

| CULTURE | STRAIN | TIME OF DAY | HOURS IN FIXING FLUID | FIXING FLUID | QUALITY OF FIXATION | POLLEN GRAINS COUNTED | PERCENTAGE GOOD POLLEN* |
|---|---|---|---|---|---|---|---|
| 68.1... | E | 3:30 P.M. | 3 | Bouin modified | Excellent | 350 | 90.3 |
| 68.9... | E | 11:30 A.M. | 4 | " " | " | 492 | 91.9 |
| 68.9... | E | 12:30 A.M. | 7 | " " | " | 543 | 85.2 |
| 68.1... | E | 10:45 A.M. | 6 | " " | " | 137 | 74.3 |
| 68.1... | E | 1:45 P.M. | 6 | " " | " | 260 | 85.0 |
| 68.9... | E | 1:30 P.M. | 5 | Bouin | Good | 129 | 84.9 |
| 68.4... | E | 1:45 P.M. | 28 | Chromo-acetic | " | 490 | 86.0 |
| 68.4... | E | 12:5 P.M. | 24 | Strong Flemming | Excellent | 114 | 82.5 |
| 68.1... | E | 10:00 P.M. | 24 | " " | " | 168 | 92.3 |
| 68.1... | E | 2:00 A.M. | 8 | Bouin modified | Very good | 182 | 81.9 |
| 68.1... | E | 12:00 A.M. | 7 | " " | Excellent | 351 | 92.4 |
| 68.5... | E | 2:45 A.M. | 26 | Weak Flemming | Very good | 108 | 86.4 |
| 63.6... | For-mosa | 11:35 A.M. | 5 | Bouin modified | Excellent | 220 | 89.5 |
| 63.8... | " | 11:00 A.M. | 7 | " " | " | 645 | 89.2 |
| 63.8... | " | 4:15 P.M. | 3 | " " | " | 320 | 87.4 |
| 63.6... | " | 3:40 P.M. | 4 | " " | " | 214 | 82.5 |
| 63.7... | " | 1:45 P.M. | 5 | " " | " | 113 | 83.5 |
| 63.7... | " | 10:15 A.M. | 7 | " " | " | 108 | 83.9 |
| 610.3... | C | 12:20 A.M. | 6 | Bouin modified | " | 64 | 93.4 |
| 610.3... | C | 3:00 P.M. | 24 | Strong Flemming | " | 78 | 76.2 |
| 610.3... | C | 12:10 A.M. | 6 | Bouin modified | " | 213 | 93.5 |
| 610.3... | C | 11:45 A.M. | 24 | Strong Flemming | " | 420 | 91.8 |
| 610.4... | C | 4:20 P.M. | 24 | " " | " | 205 | 82.9 |
| 610.3... | C | 1:00 P.M. | 6 | Bouin modified | " | 94 | 78.0 |
| 610.3... | C | 1:35 P.M. | 5 | " " | " | 150 | 84.7 |
| 610.1... | C | 12:45 P.M. | 24 | Weak Flemming | Very poor | 108 | 92.0 |
| 69.4... | M | 11:35 A.M. | 5 | Bouin modified | Excellent | 345 | 91.2 |
| 69.4... | M | 4:30 P.M. | 3 | " " | " | 219 | 90.5 |
| 69.4... | M | 2:30 P.M. | 5 | " " | " | 235 | 93.2 |
| 69.4... | M | 12:55 P.M. | 6 | " " | " | 400 | 90.1 |
| 69.2... | M | 1:10 P.M. | 7 | " " | " | 139 | 63.0 |
| 69.5... | M | 1:20 P.M. | 4 | " " | " | 321 | 87.8 |

* Average percentage of good pollen in strain E was 85.2; in mut. *formosa*, 86.00; in strain C, 86.5; and in strain M, 85.8.

11 μ, were cut and stained in iron-alum haematoxylin, which proved excellent for the sharp differentiation of the nuclear structures. All the important and critical stages in the development of the pollen were plentifully obtained from the various individuals from which the fixations were made.

## MEIOSIS IN O. PRATINCOLA STRAIN E

MITOSES IN ARCHESPORIUM OF ANTHER.—The mitoses in the archesporium of the anthers of *Oenothera pratincola* strain E, conform generally to the account of *O. grandiflora* Solander given by DAVIS (**22**), and hence only the critical stages will be discussed.

Differentiation of the archesporium in the anthers of *O. pratincola* takes place at a very early period. Cells divide both lengthwise and crosswise during its development, and finally a single and sometimes a double row becomes transformed into pollen mother cells. Numerous nuclear divisions take place at the same time in various regions of the anther.

The sporophytic mitosis is best studied in the final mitoses of the archesporial cells, which generally convert the primary single row of cells into a double row that later becomes the pollen mother cells. The somewhat greater size of the nuclei, as compared with the nuclei of the other cells of the developing flower, facilitates accurate observation.

The diploid chromosome number in *O. pratincola* strain E and mut. *formosa* is fourteen, as usual for species of *Oenothera*. This can be seen clearly in the nucleus before the appearance of the spindle fibers prior to the metaphase of the last division in the archesporium. The chromosomes at this time appear as variously bent rods, as shown in the polar view of the equatorial plate presented in fig. 1. During the metaphase and the early anaphase the chromosomes assume the forms of thick U's and V's, due to condensation (fig. 2). In the late anaphase and with the approach of telophase, condensation proceeds still further. Because the chromosomes are so closely massed during the stages of late telophase, it was impossible to determine whether they undergo a definite lengthwise split into two parallel threads, as claimed by DIGBY (**30**) for *Osmunda* and FRASSER and SNELL (**35**) for *Vicia faba*, or whether they become irregularly alveolized and form together a continuous reticulum, as described by SHARP in *Vicia* (**75**) and *Tradescantia* (**76**). The nuclei then pass into the resting condition preliminary to meiosis, in which the outlines of individual chromosomes become entirely lost.

RESTING NUCLEUS BEFORE MEIOSIS.—The nuclei of the pollen mother cells pass through a relatively long period of rest before the

advent of the prophase of the heterotypic division. They measure 9–11 μ, and possess a prominent nuclear membrane. The most conspicuous structures in the nucleus at this time are the nucleoli, frequently three or four in number and sometimes as many as five and six. Only one of these bodies attains a large size (fig. 3), however, and sometimes a shining area resembling a vacuole may distinctly be observed within it. The large nucleolus is nearly spherical, and lies toward the center of the nucleus. The smaller nucleoli are scattered in the nucleus, and seem to have no definite positions. It is difficult to determine the exact number of nucleoli, since some of them are as small as the larger chromatin granules. Certain of the smaller nucleoli are frequently seen lying beside the largest, and these probably unite with the latter, as reported by GATES (43) in the case of *O. rubrinervis*.

During the resting stage the nucleus contains a chromatic reticulum of delicate single threads, evenly distributed through its interior (fig. 3). Very small chromatin granules may be seen irregularly scattered over these threads. At the juncture of two threads chromatin granules of varying shapes and sizes were distinctly observed. These fine threads run through peripheral regions of the nucleus and over the surface of the nucleolus, and are in direct contact with the chromatic material in the nucleolus (fig. 3). The threads are uniformly single and show no parallelism.

PRESYNIZESIS STAGES.—Shortly before the resting nuclei enter the prophase of the heterotypic mitosis, some parallelisms in the threads of the reticulum may be observed, but these are not numerous and seem not to be significant. It is quite natural that some parallelisms among the threads should exist, taking into consideration their number within so small a space. At the approach of the heterotypic prophase the threads of the reticulum begin to thicken and to contract gradually, and many of them unite with one another in an irregular manner. This process transforms the characteristic fine-meshed reticulum of the resting stage (fig. 3) into an open reticulum, the threads of which are coarser and rougher (figs. 4, 5). The union of threads with subsequent condensation which effects the transformation of a delicate reticulum into a system of coarse and rough threads, varying in diameter, is a gradual process (fig. 6).

While this is taking place, there may still be observed in the nucleus some delicate threads not yet thickened; and also some shriveled threads may be observed which appear to be in the process of delivering their chromatin content to the threads that are to survive. The chromatin accumulations that are scattered irregularly throughout the nucleus during the resting stage probably become amalgamated with the thickening threads, and even if they exist their presence is not recognized with certainty. The pull exerted on the peripheral threads, due to the contraction, shrinkage, and condensation of the internal threads, causes them to draw away from the nuclear membrane and they come to lie in a tangled mass at one side of the nucleolus, giving the characteristic stage of synizesis. Occasionally the threads very close to and connected with the nuclear membrane may still be seen in place, but they are not smooth and continuous (fig. 6). The nucleolus leaves its central position in the nucleus and moves to the periphery, where it generally lies flattened against the nuclear membrane, next to the contracted mass of threads (fig. 7).

Some parallelism among the threads may be observed at times during this process of condensation; but since the process is one of contraction, it is to be expected that threads will occasionally be drawn into side-by-side relations which are not to be regarded as significant.

The transformation of the fine-meshed reticulum, composed of single delicate threads with scattered chromatin granules of varying shapes and sizes, into a reticulum of rather large meshes, composed of threads of coarser and rougher nature, forming a spireme, has given rise to much discussion among prominent cytologists as to the method by which this transformation is brought about. Two interpretations have been offered for various material. One is supported by GRÉGOIRE (**50, 51**), ALLEN (**1**), ROSENBERG (**69, 70, 71**), STOMPS (**85**), and others and the other interpretation is held by FARMER and MOORE (**33, 34**), DIGBY (**28, 29, 30**), MOTTIER (**65, 66, 67**), FRASER and SNELL (**35**), FRASER (**36**), and their followers. Both schools agree that the most important event of this process in most material is a side-by-side association of threads during the earlier part of the prophase, but the two schools offer very different inter-

pretations of the history. The first interpretation, that of parasynapsis, holds that the two threads are homologous spiremes, one derived from the egg and the other from the sperm. These threads hold two sets of chromosomes, and their association gives rise to a bivalent spireme. The second interpretation, that of telosynapsis, maintains that the double thread when present is due to the lengthwise division of chromosomes during telophase, or even anaphase of the previous mitosis, and consequently does not represent an association of two spiremes of different descent. By the interpretation of telosynapsis, double threads, if found during the prophase, are merely associations of daughter spiremes.

The history of meiosis in *Oenothera pratincola* and all its strains favors the telosynaptic interpretation.

## Synizesis

The thickening of the threads goes on for some time, due to contraction, and also because material is received from the chromatin granules and the other threads (fig. 6). Some of the threads become very thin, and certain of them become quite shriveled as their material presumably passes into the developing spireme. Certain parts of the threads near the nucleolus become gorged with material, appearing much swollen. Material from the nucleolus is apparently received by the nearest threads more rapidly than it is dispersed, and consequently parts of the threads become much thickened. The reticulum at this stage (fig. 6) shows a spireme composed of rather thick and uniform threads, some of which may be followed for a considerable distance in the tangled mass. The nucleolus loses its spherical shape and becomes somewhat flattened against the nuclear membrane. It is quite empty of chromatic material, as is seen by its reaction to the stain; but the endonucleolus is clearly seen as a very small round body taking the stain conspicuously (fig. 9). The spireme becomes more closely contracted, and finally has the appearance of a closely wound ball of threads, the synizetic knot (fig. 8). The knot remains in this much contracted condition of mid-synizesis for a long time, while the threads of which it is composed become more uniform in thickness and longer. The process of transformation from a reticulum of delicate threads into the spireme

that emerges at the end of synizesis takes place very slowly; in fact, synizesis is of longer duration than any other period in the development of the pollen. During certain stages the knot becomes so dense that it is impossible to determine with certainty what is happening within.

### Open spireme

After some time the knot gradually begins to loosen, probably due to the lengthening of the threads. Many small loops of various sizes begin to extend from the periphery of the knot, while the greater portion of it is still so contracted that nothing of its structure can be distinguished with accuracy (fig. 9), although it is clear that it is composed of thicker threads. The loops on the periphery of the knot loosen while the central mass of threads is still drawn together in a very complicated manner (fig. 10). Sometimes during this stage the threads are so thick and full of chromatin that it is very hard to recognize them as threads. Finally they become uniform and those in the center loosen sufficiently to reveal their individuality. During no stage is the spireme entirely clear and free from chromatin accumulations, however, but differential staining shows it to be composed of distinct threads much swollen and gorged with material (fig. 11). During this emergence of the spireme from the contracted condition of mid-synizesis the threads become distributed uniformly throughout the nucleus. Some of them become very prominently beaded, the beads being placed in a single row, and these are probably the chromomeres of various authors (fig. 12). It is possible to trace a single thread for some distance as it winds about in the nucleus. No threads with free ends were found in this stage.

The nucleolus which lies flat against the nuclear membrane throughout synizesis and during the emergence of the open spireme later takes on a spherical form, and generally moves to the center of the nucleus. It is quite homogeneous and free from chromatic material, as indicated by its failure to stain; but the minute, deep-staining endonucleolus within may be distinctly observed (figs. 12, 13, 15).

The spireme has been carefully studied for evidence of double structure but none has been found; the threads are everywhere uniformly single.

During synizesis and the stages of the open spireme the pollen mother cells become round and separate from one another. In the stages prior to synizesis they are packed closely together and consequently are angular.

### Second contraction

After remaining for some time in the open spireme stage, the nucleus enters the stage known as the second contraction. This stage is of relatively short duration. The threads that were rather widely and evenly distributed during the open spireme stage begin to contract, with accompanying condensation of chromatic material. The process of contraction and condensation takes place rapidly, and consequently the threads at the periphery come to form radiating loops from the central mass (fig. 13). The threads in the center become much swollen and form large irregular masses of chromatin (figs. 14, 15). The individual threads appear to be lost in the central mass, but differential staining shows this chromatic mass really organized, consisting of closely contracted and much thickened threads (fig. 13). It was not possible to determine whether these central threads unite with one another as they come to lie in a mass, but close observation indicates that they are distinct and separate, although very much swollen (figs. 14, 15).

As condensation proceeds, the material from the radiating loops is drawn to the center, and at the time of the greatest contraction the contents of the nucleus look like an irregular mass of chromatin with very slight traces of loops at the periphery. In no case, however, are these loops lost during any stage of second contraction. As the loops become shorter and shorter their two sides approach, until in some cases they actually come to lie against each other. Very soon there appear constrictions in the loops, which probably indicate segment of the spireme that are to become the chromosomes. Some loops are made up of only one chromosome (fig. 14), while others may have as many as two or three (fig. 15). After some time the outlines of the chromosomes become clear. While some of them may be distinguished clearly in one part of the contracted mass, it frequently happens that in other parts definite organization cannot be recognized (fig. 15). The formation of the chromosomes through segmentation of the spireme is easily demonstrated.

A most careful study failed to show any evidence of lengthwise fission among the loops in the spireme during the second contraction; the spireme was found to be univalent in nature, the threads being everywhere single. A split in the spireme would be expected if it were bivalent, since it is at this stage that the chromosomes prepare to separate from each other; therefore it is certain that each of these loops represents one or more chromosomes attached end to end.

The nucleolus, during the stage of second contraction, generally lies against the nuclear membrane, and is oval in form with little or no stainable material. In some nuclei it comes to the center. The endonucleolus may be observed at this stage as a black body inside the nucleolus (figs. 13, 15), which is not at all involved in the processes of second contraction.

### Final prophase stages

Ordinarily in plants and animals the term diakinesis is used to denote the stage when the paired homologous chromosomes lie in the nucleus prior to the formation of the heterotypic spindle. It is doubtful whether this term should be used at all in the case of *Oenothera pratincola*, which shows no pairing but a closed chain of fourteen chromosomes attached end to end. During the prophase stages so far discussed there is little opportunity for studying the individual chromosomes, because of the complexity of the stages through which they pass, and also due to the fact that they are not in a compact form; but from now on stages will be dicussed in which individual chromosomes are clearly shown.

At the end of the second contraction there emerge gradually chromosomes, irregular in outline and connected end to end by delicate threads. They sometimes lie over one another in a confused mass, and frequently their arrangement cannot be determined with accuracy (fig. 16). Later they become more evident with the loosening of the contracted mass (fig. 17). Shortly after this stage the whole situation clears, and a very striking arrangement of the fourteen chromosomes attached by delicate threads end to end in a closed chain is readily observed (figs. 18–20). Sometimes an attachment breaks and instead of a closed chain of fourteen chromosomes an

open chain results (fig. 21). It is difficult, because of the length of the chain of chromosomes and because of its loops, to find sections in which all the members are present, all the attachments undisturbed and perfectly clear. I have examined nearly one thousand cells in this species and found no case of chromosomes in a paired side-by-side arrangement. The results of a critical examination of the nuclei at this stage are summarized in table II. Although many nuclei had been cut, so that certain chromosomes were missing,

TABLE II

ARRANGEMENT OF CHROMOSOMES DURING LATE PROPHASE IN OENOTHERA PRATINCOLA

| ARRANGEMENT | NUMBER OF NUCLEI OBSERVED |
|---|---|
| Closed chain of fourteen chromosomes | 37 |
| Open chain of fourteen chromosomes (attachment broken at one point) | 17 |
| | Total 54 |
| Thirteen chromosomes in chain, one missing | 19 |
| Twelve chromosomes in chain, two missing | 31 |
| Eleven chromosomes in chain, three missing | 44 |
| Ten chromosomes in chain, four missing | 58 |
| Nine chromosomes in chain, five missing | 35 |
| Eight chromosomes in chain, six missing | 30 |
| | Total 217 |
| | Total 271 |

the observations uniformly showed that all the chromosomes present were in a continuous chain or ring.

This final stage of the heterotypic prophase lasts only for a short time. The nucleolus, pressed against the nuclear membrane, quite free of the chromatic material, disappears slowly. The deep-staining endonucleolus persists even after the disappearance of the nucleolus (fig. 23).

### HETEROTYPIC METAPHASE

The nuclear membrane breaks down slowly. Its dissolution is first indicated by the surrounding cytoplasm becoming rather dense and by the development of delicate fibrils. The fibrils are at first scattered without order. When the nuclear membrane has complete-

ly dissolved they appear to penetrate the nuclear cavity, and very soon a multipolar spindle is formed with the fibers arranged in cones (fig. 23). The fibers enter the cluster of chromosomes in an irregular and complicated manner. The chromosomes, which have an irregular outline during the final stages of prophase, change in shape and size with condensation, becoming quite compact, when they look like thick V's and rods. The closed chain of fourteen chromosomes still persists (fig. 22), except when occasionally a delicate attachment breaks and an open chain results (fig. 23). The endonucleolus may be observed even at this stage, but with the approach of anaphase it disappears.

The multipolar spindle becomes bipolar, and the chromosomes, still in a closed chain, pass to the equatorial region of the spindle. Shortly after, the spindle fibers, which by this time are organized into clusters, attach themselves to the mid-region of the V-shaped chromosomes in such a way that the alternate chromosomes go to the same pole (fig. 24). Some of the chromosomes are rod-shaped, in which case the spindle fibers are attached to their ends. In view of the fact that all the fourteen chromosomes are attached to one another end to end in a chain, which is sometimes very much looped, it is difficult to obtain a clear view of all the chromosomes and their attachments. In spite of these difficulties, a thorough study was made of the best nuclei at this stage, so as to determine the exact nature of the attachments of the spindle fibers to the chromosomes. Only the nuclei presenting a clear view of all the fourteen chromosomes with their attachments have been included in this survey, a summary of which is given in table III. Hundreds of cells have been examined in which some of the chromosomes were missing but the attachments present were intact; these have not been included in table III.

The data presented in table III clearly show that the arrangement of the chromosomes in many nuclei during the heterotypic metaphase is zigzag. As a result of such an arrangement, alternate chromosomes go to the same pole in the species under discussion. Certain irregularities in the zigzag arrangement do occur, however, the percentage of which is greater in this strain than in *O. biennis* and "*O. muricata*," as reported by CLELAND (**18, 19**). It is 30.1 per cent for *O. pratincola* strain E. The irregularities may conveniently

be listed under the following headings: (1) Two chromosomes in different parts of the chain are suspended between the poles (fig. 25 *a*, *b*). If both of these go to the same pole, the distribution will be eight chromosomes to one nucleus and six to the other. In case they go to different poles the distribution will be seven chromosomes to each nucleus. (2) Two adjacent chromosomes in one part of the chain are attached to the spindle fibers leading them to the same pole; and in the other part of the chain a corresponding pair is similarly attached to fibers that lead them to the other pole (fig. 26 *a*, *b*). In

TABLE III

RESULTS OF SURVEY OF CELLS DURING HETEROTYPIC METAPHASE SHOWING CHROMOSOME ARRANGEMENT

| CHROMOSOMES ALL DISTINCTLY VISIBLE AND END-TO-END ATTACHMENT CLEAR | NUMBER OF NUCLEI OBSERVED |
|---|---|
| Closed chain of fourteen chromosomes complete and regularly zigzag | 135 |
| Open chain of fourteen chromosomes complete and regularly zigzag | 39 |
| | Total 174 |
| Closed chain of fourteen chromosomes complete and attachments irregular | 43 |
| Open chain of fourteen chromosomes complete and attachments irregular | 32 |
| | Total 75 |
| | Total 249 |

this type of irregularity, however, the number of chromosomes going to the two poles will be equal, seven to each pole. (3) A pair of adjacent chromosomes is drawn to the same pole, while a chromosome is uncertainly suspended in the equatorial region (fig. 27 *a*, *b*). This chromosome might go to either pole. If it is drawn to the pole with the abnormally placed pair, the number of chromosomes passing to that pole will be eight and the other pole will then have only six chromosomes. All these irregularities have been noted by CLELAND (18, 19) for *O. biennis* and "*O. muricata*." (4) Three or sometimes four chromosomes in a group have fiber attachments of such a nature that it is impossible to predict the number that might go to the two poles (figs. 28–30).

Careful observation during mid-interkinesis following the hetero-

typic mitosis also gives some idea of the irregularity in the chromosome distribution. Nine hundred nuclei in this stage were examined, of which ninety-four were found to have eight or six chromosomes, which is an irregularity of 9.4 per cent. Since irregularity in the zigzag arrangement during metaphase is not necessarily the only cause of abnormal distribution (six and eight) of the chromosomes, the total percentage of irregularities is higher, and was actually found to be about 30.1 per cent.

### Heterotypic anaphase and telophase

In early anaphase the chromosomes present the zigzag arrangement (fig. 24) which is so clearly described and illustrated by Cleland in all his papers on the cytology of *Oenothera*. The chromosomes separate during anaphase into two sets, breaking their connection with each other. Presently they reach the two poles of the spindle, seven passing to each pole when the distribution is regular (fig. 31), and eight to one pole and six to the other if the distribution is irregular (fig. 32). Soon after the chromosomes reach the pole they generally form a small star-shaped cluster, with one chromosome in the center and six at the periphery, an arrangement typical of species of *Oenothera* at this stage (fig. 33). After some time the chromosomes split lengthwise (fig. 34), the split at first not being conspicuous. The chromosomes spin out delicate threads which generally connect them with one another. A vacuole-like space appears around the group of chromosomes, and the outer boundary of this area marks the nuclear membrane.

### Interkinesis

The slender threads connecting the chromosomes become hazy during the interkinesis and the nuclei enlarge rapidly. The chromosomes also enlarge and become irregular in form. Shortly after this the split in the chromosomes becomes conspicuous, and the halves frequently separate to give an irregular X (fig. 35). These halves or daughter chromosomes are loosely connected in their middle region. In certain cases the chromosomes come to show denser regions within, which stain more deeply than the main body of the chromosomes (fig. 35).

During this stage one or more nucleoli appear at first as minute globules, in connection with chromosomes. Sometimes they are associated with the chromatin threads that pass between the chromosomes (fig. 34). It appears that they arise *de novo*, as there is nothing to indicate their survival from previous stages.

### Homeotypic division

The daughter chromosomes which arise from the lengthwise division of the heterotypic chromosomes condense during the prophases and finally appear as short rods (fig. 36). As soon as the nuclear membrane breaks down, the spindle fibers become conspicuous and enter the nuclear cavity. Very soon a multipolar spindle is formed, which later becomes bipolar, and the chromosomes pass to the equatorial region of the spindle (fig. 37). The fibers, which are organized by this time into thick clusters, attach themselves to the perfectly paired daughter chromosomes. Shortly after this the daughter chromosomes separate and pass to the poles, seven chromosomes in each set. The homeotypic division is normal except where there has been an irregularity in the preceding heterotypic mitosis, in which case eight and six chromosomes respectively may be distributed instead of the normal seven (fig. 36).

The four groups of chromosomes resulting from the homeotypic division lie rather close together in the pollen mother cell. Shortly, a clear hyaline space resembling a vacuole arises around each group. The outer boundary of this vacuole ultimately becomes the nuclear membrane. The nuclei then enlarge rapidly, the chromosomes gradually becoming long and irregular in form, and they spin out delicate threads which later become irregularly thickened. Gradually the chromatin material from the chromosomes becomes located in these threads. The outline of the chromosomes may still be recognized at this stage, but as the dispersion of the chromatin proceeds the boundaries of chromosomes can no longer be recognized. Secondary threads arise from the primary threads, and the chromatic material passes rapidly into them. Finally the nucleus becomes filled with a network of irregularly thickened threads, as shown in fig. 38. Later, one or more nucleoli appear together with chromatin granules of varying shapes and sizes.

### Meiosis in O. pratincola mut. formosa

The nuclei of the pollen mother cells in mut. *formosa* during all the stages of meiosis and the following division resemble those in *O. pratincola* strain E.

### Meiosis in O. pratincola strain C

The history of meiosis in strain C resembles that of strain E and mut. *formosa* in all respects. Careful observations were made on hundreds of nuclei of the pollen mother cells in this strain, in the hope of discovering some peculiarities distinguishing it from strain E and from mut. *formosa*, but nothing different was found. It may be stated confidently that if the slides of strain E, strain C, and mut. *formosa* were mixed it would be impossible to distinguish them.

### Meiosis in O. pratincola strain M

It will be remembered that strain M is the cross mut. *formosa* pollinated by f. *typica* of strain C. It has the appearance of *O. pratincola* f. *typica*, the flat-leaved character of which dominates the revolute-leaved character of mut. *formosa*. The $F_1$ plants cannot be distinguished from strains E and C of *pratincola*, therefore, although they carry the revolute-leaved character of mut. *formosa* as recessive.

When self-pollinated, strain M gives an $F_2$ progeny showing simple monohybrid segregation of 3 typical *pratincola:* 1 mut. *formosa*. The strain was designated M by BLANCHARD (COBB 21) because of the Mendelian segregation.

All the stages in the course of meiosis in strain M show clearly that there are no fundamental differences between this form and the other strains discussed up to and including the second contraction. With the unfolding of the irregular threads of the second contraction, however, an entirely new situation is presented. All the strains discussed before show chains of fourteen chromosomes attached end to end in the later stages of prophase. Strain M has a closed chain of twelve chromosomes attached end to end, to which is linked a pair of chromosomes in the form of a ring (fig. 41 *a*). In the earlier periods of metaphase the ring of two chromosomes remains attached to the circle of twelve (figs. 42 *a*, 43 *a*), but during the late metaphase it breaks away and takes a position at one side of the spindle

(fig. 44 *a*). The chromosomes assume the form of thick V's and rods, due to condensation. The characteristic zigzag arrangement is clearly shown in the closed chain of twelve chromosomes, alternate chromosomes passing to the poles of the spindle. The chromosomes of the detached pair separate and accompany the two groups of six chromosomes as they pass to the poles. The chromosomes from the pair may be followed into late anaphase, but with the approach of the telophase each becomes associated with the other six chromosomes, and it is impossible to distinguish them. The pair of chromosomes is significant of the genetic behavior of strain M. These homologous chromosomes probably carry respectively the genes for flat leaf (*pratincola*) and revolute leaf (*formosa*), and their segregation and recombination in the breeding of strain M accounts for the simple Mendelian ratio peculiar to this monohybrid. The remaining stages of pollen formation in this plant are the same as those described in *Oenothera pratincola* strain E.

### Formation of pollen grains

The four microspore nuclei grow rapidly and delicate fibers appear between them. These sometimes become prominent (fig. 45), resembling spindle fibers, but they soon disappear. Shortly small refractive vacuoles begin to develop in the cytoplasm (fig. 46). These are numerous at first, and distributed rather uniformly through the cytoplasm of the pollen mother cell. The regions of the mother cell between the nuclei infold at the periphery (fig. 46), nearly equidistant from the nuclei and at right angles to the former spindles; so that when the new walls are developed the resulting spores are tetrahedral in form. Later, vacuoles become arranged in the cytoplasm between the nuclei and enlarge, some of them fusing to form large flattened vacuoles (fig. 47). They finally become plates which extend from the center of the cell between the nuclei to the infolded regions at the periphery. The complete cleavage of the protoplasmic material appears to result from the furrows originating at the surface (fig. 48), which grow inward very rapidly, breaking through the large vacuoles. The furrows are thin at first but later become wider and conspicuous.

C. H. FARR (37, 38, 39, 40) has shown that the simultaneous divi-

sion of the pollen mother cells in *Nicotiana*, *Magnolia*, *Sisyrinchium*, and *Nelumbo* occurs by means of furrows. Before this time it was thought that the quadripartition was brought about in conjunction with cell plates formed between spindles. W. K. FARR (41) also reports a similar process in *Coboea*, and CASTETTER (12, 13) for *Melilotus* and *Cucurbita*. CLELAND (15, 16, 18, 19) has noted an invagination process, which he does not fully describe, in *Oenothera franciscana*, *O. biennis*, *O. biennis sulfurea*, and "*O. muricata*." The present studies on *Oenothera pratincola* agree with his observations so far as he records them. He does not refer to the vacuolation which precedes the final wall formation.

A membrane appears very soon around each young microspore, first recognized as a delicate film lining each cell cavity of the tetrad. It is distinct from the wall of the pollen mother cell although in most intimate contact with it; this membrane presently thickens. The young pollen grain is bluntly tetrahedral, with the peripheral side infolded to form a basin. The cell cavity is densely filled with protoplasm and there are no large vacuoles. The concavity of the basin is directed toward the apex of the tetrahedron. The wall is extremely thin at the three peripheral angles of the pollen grains. Shortly it thickens considerably and a mucilaginous material develops at these three angles. The little disks of mucilage enlarge and extend somewhat laterally. FRITSCHE introduced the name "Zwischenkörper" for these mucilaginous disks, and the same name has been used by NÄGELI and STRASBURGER. BEER (7) calls them interstitial bodies. The normal pollen grains of *O. pratincola* have three of these interstitial bodies. Some have only two and still others have only one. These cases are probably abnormal. The pollen grains of *gigas* forms of *Oenothera* have four or more of these disks. Very soon the wall of the pollen mother cell breaks down and the pollen grains are set free. As the pollen grain enlarges, the three interstitial bodies become more and more prominent, finally becoming three lobes. This gives the peripheral face of the pollen grain a more pronounced triangular appearance. Shortly a secondary thickening develops within the first pollen wall, extending over the whole of the inner face of the pollen membrane but very thin at the three lobes. A disk-like partition is formed across the base of each lobe. This disk con-

sists of two parts, the outer part a dense homogeneous layer and the inner part a less dense stratified lamella which is cap-shaped. The cavities of the three lobes at this stage no longer contain the mucilaginous substance which earlier takes a brilliant stain with haematoxylin. BEER (7) suggests that this mucilaginous substance is used in the formation of the closing disks. He thinks that the closing disk is later eaten away by a solvent, probably an enzyme secreted by the protoplast. The thickening of the pollen wall continues in the regions between the lobes. My observations on the development of pollen in *O. pratincola* are in accord with those of BEER for *O. biennis* and *O. longiflora*.

## Cytological discussion

The conclusions of GATES (**42, 43, 46**), DAVIS (**22, 23, 24**), GEERTS (**48**), CLELAND (**15, 16, 18, 19**), VALCANOVER (**88**), and HÅKANSSON (**53**) are all in substantial agreement that the arrangement of the chromosomes in *Oenothera* is telosynaptic. Only one investigator, BOEDIJN (**9, 10**), maintains it to be parasynaptic, and his observations are at variance with those of the investigators just cited. BOEDIJN reports for *Oenothera lamarckiana*, during the early part of the heterotypic prophase, the side-by-side conjugation of the thick threads. From this stage he passes to the stage known as the second contraction, and figures pairs of long slender threads (two chromosomes) twisted in such a manner as to give the appearance of normal strepsinema stage. In early diakinesis stages he observed seven pairs of chromosomes, often entirely separate from one another and sometimes forming rings, and states that the single chromosomes comprising these pairs may split partially during this stage. SINOTÔ (81) reports the pairing of homologous chromosomes in *O. lamarckiana*. He does not think that they are parasynaptically arranged (82) after the beginning of the prophase in *O. sinuata* L. CLELAND (17) finds in *O. lamarckiana* at diakinesis a circle of twelve chromosomes and a ring of two, in contrast to the seven pairs described by BOEDIJN at this stage. GATES (**42**), GEERTS (**48**), DAVIS (**24**), and HÅKANSSON (**53**), who have also worked on the cytology of *O. lamarckiana*, do not report any evidence that would lead one to believe in the parasynaptic interpretation proposed by BOEDIJN.

It is worth noting here that some genera related to *Oenothera* have been stated to show parasynaptic arrangement of the chromosomes. TÄCKHOLM (**86**) for *Lopezia*, MICHAELIS (**64**) and SCHWEMMLE (**72**) for *Epilobium*, HÅKANSSON (**52**) for *Godetia*, and SCHWEMMLE (**73**) for *Eucharidium* report parasynapsis. SCHWEMMLE (**72**) reported telosynapsis in *Oenothera*, but changed his interpretation through conclusions reached in a cytological study of *Eucharidium concinnum* (**73**). He describes for *Eucharidium* three methods of gemini formation, one of which (Reihe C) resembles that of *Oenothera* in some stages. His figures, apparently of second contraction (figs. 27–29, Taf. V), resemble those of CLELAND for this stage (**15** figs. 15, 21; **16** fig. 5). The interpretations put on apparently similar figures by the two investigators, however, are different. CLELAND and others believe that the chromosomes that emerge from second contraction result from the segmentation of a univalent spireme. SCHWEMMLE, on the contrary, maintains that during the second contraction the chromosomes are already in pairs. He gives some figures (figs. 2–5, 12–14, 20–22) of the stages prior to second contraction. These stages are critical for the determination of telosynapsis or parasynapsis in any species. None of these figures resembles the stages that I have observed in *Oenothera pratincola*, nor do they resemble the figures of other investigators of *Oenothera* cytology, with the possible exception of certain of BOEDIJN'S (**10**) figures of the early prophase. The reported absence of these stages in *Oenothera*, which according to SCHWEMMLE determine telosynapsis or parasynapsis, is believed by him to be due to environmental conditions, such as temperature and other undecided factors, which suppress their appearance. He suggests that as a result of these conditions the normal development of the anther and the pollen mother cell is in some cases retarded and in other cases prolonged. He predicts that it may become possible to demonstrate parasynapsis in *Oenothera*. It must be remembered that *Eucharidium* and *Oenothera* are distinct genera, and that conclusions for *Oenothera* through a study of *Eucharidium* may not hold good for the former.

In a recent paper, SCHWEMMLE (**74**) reports on the cytology of the cross *Oenothera berteriana* × *Oenothera* (*Onagra*) "*muricata*." Both parents have fourteen chromosomes, but those of the latter are twice

as large as those of *berteriana* (as observed during the early anaphase). All the stages of meiosis in this hybrid, from the heterotypic prophase to the untangling of the second contraction, are similar to the stages usually met in the meiosis of species of *Oenothera*. At diakinesis the chromosomes of "*O. muricata*" form a closed chain, as shown by CLELAND (19); the arrangement of the chromosomes in *O. berteriana* at this stage is not known. SCHWEMMLE states that the hybrid shows great variation in the arrangement of the chromosomes at diakinesis. He reports in some nuclei two small chains of three chromosomes arranged end to end, a pair of chromosomes, and six single chromosomes; in other nuclei many pairs; and in still others chains of chromosomes of large number accompanied by fewer univalent chromosomes. Cases of small chromosomes pairing with large ones are also reported by SCHWEMMLE. When the nuclear membrane dissolves, prior to metaphase of the heterotypic mitosis, six of the larger chromosomes of "*O. muricata*" may be recognized; but the seventh is not to be clearly seen (74). The small chromosomes of *O. berteriana* are likewise seen at this stage. The arrangement of the paternal and maternal chromosomes on the spindle at the heterotypic metaphase is variable. During the late metaphase, when some of the chromosomes have nearly reached the pole, others are seen lagging in the mid-region of the spindle. The distribution of the chromosomes to the two poles during anaphase is also variable. SCHWEMMLE observes the following cases: (1) four large three small to one pole and three large four small to the other; (2) five large two small to one pole and two large five small to the other; (3) six large one small to one pole and one large six small to the other; (4) seven large to one pole and seven small to the other. He finds abundant spindles with unequal chromosome numbers at anaphase, resulting in irregular distribution of the chromosomes to the two poles. He suggests that this irregularity is due to the fluctuations of the autumnal temperature when the material was fixed. He concludes that in a cross between two species of *Oenothera* presenting size differences in the chromosomes, the paternal and the maternal can be recognized and their distribution during meiosis observed.

The four strains under discussion, *O. pratincola* f. *typica* strain E, mut. *formosa*, f. *typica* strain C, and strain M, have been care-

fully examined and the arrangement of the chromosomes in all of them was found to be telosynaptic. All these strains will be treated together in this discussion because they show the same characteristic behavior. During the stages of the early heterotypic prophase there is hardly any evidence suggestive of parasynapsis. When the threads thicken and contract some of them may be found side by side, but such chance parallelism is to be expected. By careful and detailed observations it becomes evident that the formation of the spireme in the heterotypic prophase is effected by an irregular process of condensation, rather than by a side-by-side approximation of two distinct thread systems. During the open spireme stage following synizesis the threads are uniformly single, and there is no evidence of a bivalent spireme. During the second contraction following the open spireme stage, when the chromatin threads are thrown into radiating loops, these loops are also univalent. The most significant evidence that the chromosome arrangement in these strains is telosynaptic is presented with the unfolding of the chromatin threads at the end of the second contraction, from which emerges a closed chain of chromosomes attached end to end. There is no doubt that this chain is the outcome of the segmentation of the spireme at the termination of the second contraction stage.

The arrangement of the chromosomes in closed chains at the end of the second contraction stage, together with the extreme regularity with which all the stages are executed, leads CLELAND to conclude that the delicate threads of the resting nucleus in the species of *Oenothera* which he has investigated give rise to chromosomes definitely placed end to end and not to chance arrangements.

In most plants and animals the homologous chromosomes at the stage termed diakinesis are distributed in pairs throughout the nucleus. In *Oenothera* the situation at this stage, with the exception of a few species, is different. In most of the species of *Oenothera* which have been cytologically studied, a closed chain of some or of all of the chromosomes is found. Various types of chain formation have been described. In *O. franciscana* CLELAND (**15**) reports a closed chain of four chromosomes and five pairs; the chain of four, however, breaks into two pairs of chromosomes at the metaphase; in *O. biennis* and *O. biennis sulfurea* CLELAND (**18**) and EMERSON (**32**) ob-

served no pairing at all but two chains, one of eight chromosomes and the other of six, an arrangement which VALCANOVER (88) and KIHARA (54) confirm for *O. biennis*. In both *O. franciscana sulfurea* and *O. lamarckiana* CLELAND (16, 17) found a chain of twelve chromosomes to which is attached a ring of two chromosomes. His finding is confirmed by HÅKANSSON (53) for *O. lamarckiana*. Finally, SCHWEMMLE (72) in *O. rosea* and CLELAND (19) in "*O. muricata*" discovered a closed chain of all the fourteen chromosomes. Only in *O. blandina* and *O. deserens* has CLELAND (17) found seven independent pairs of chromosomes. SCHWEMMLE (72) also found seven independent pairs of chromosomes in *O. hookeri*.

When chains of chromosomes are present it becomes a matter of great interest to determine how the distribution of their chromosomes to the two poles takes place. CLELAND holds that the zigzag arrangement of the chromosomes at the heterotypic metaphase explains the situation. He states that in all the species of *Oenothera* he has investigated, where there are chains, the alternate chromosomes of the chains, because of their fiber attachments, generally pass to the same pole during the heterotypic metaphase, thus effecting the segregation of the homologous chromosomes. VALCANOVER (88), HÅKANSSON (53), and KIHARA (54) observed the characteristic zigzag arrangement described by CLELAND at this stage. EMERSON (32) did not see the zigzag arrangement in *biennis* as described by CLELAND, and consequently did not believe that the alternate chromosomes go to the same pole. He reported that the separation of the chromosomes is irregular. He suggested that *O. biennis* has fourteen different chromosomes instead of seven pairs of homologous chromosomes, and the chromosomes of this species are not homologous at all because they do not pair.

In all the strains of *O. pratincola* and mut. *formosa* the chromosomes are distributed to the opposite poles in the characteristic zigzag manner described by CLELAND, with occasional irregularity however. Whether such a zigzag arrangement leads to the separation of the homologous chromosomes, as assumed by CLELAND, and whether the chromosomes in *Oenothera pratincola* are homologous cannot definitely be stated for the present. In light of the genetical behavior of these strains, the maternal and paternal sets of chromo-

somes come out of meiosis as they entered the zygote. The only exceptions are due to irregularities in the zigzag arrangement. It appears from the genetic behavior, to be discussed in the following section, that all the chromosomes in *O. pratincola* are not homologous.

As discussed, a closed chain of fourteen chromosomes is formed in the final prophase stages, both in f. *typica*, strain C, and mut. *formosa*. Following a cross between mut. *formosa* (revolute leaves) and strain C (flat leaves), the $F_2$ homozygous dominant (flat-leaved) shows at this stage not a closed chain of fourteen chromosomes, but a circle of twelve chromosomes and a ring of two chromosomes attached to it. The question that presents itself is why and how the closed chain of fourteen chromosomes breaks into a closed chain of twelve chromosomes and a ring of two. An interpretation offered by Dr. F. COBB BLANCHARD is given in the genetical discussion to follow.

The nature and function of the nucleolus have been the subject of much discussion in older as well as in more recent cytological literature. Some investigators believe that the nucleolus is merely a secretion product of the nucleus. A great number of the older writers (for literature see WAGER **93**), as well as modern cytologists, such as LENOIR (**58, 59**), LITARDIÈRE (**60**), TAMURA (**87**), VAN CAMP (**89**), and many others believe, however, in the transportation theory. In *Oenothera*, CLELAND (**15, 16, 18, 19**) and BOEDIJN (**9**) support the transportation theory. SINOTÔ (**82**), working with *O. sinuata* L., finds no evidence for the transportation theory; that is, finds no evidence that the nucleolus acts as a storage structure.

The nucleus of pollen mother cells of *O. pratincola* contains at least one large spherical nucleolus. Sometimes more than one may be present. During the late synizesis some of the threads connected with the nucleolus become greatly enlarged, as though material had suddenly been transferred to them. This suggests that the nucleolus acts as a reservoir, from which chromatic substance is drawn to build up the spireme in the final stages of the heterotypic prophase. The nucleolus in the resting nucleus stains very deeply with haematoxylin, but very little of the stain is held in later stages of prophase, probably because the stainable material is carried away to build up

other structures. When the nucleolus is divested of all of its coloring matter, it shows in its interior a very small spherical body, the endonucleolus. This minute structure is sometimes connected with the spireme, but in most cases lies freely in the interior of the nucleolus. It disappears during the late metaphase. During interkinesis many nucleoli develop in contact with the chromosomes, arising always *de novo;* hence it appears highly probable that the nucleolus is a storage organ for material, akin to chromatin, which is formed anew in each nucleus.

The segmentation of protoplasm by cleavage furrows was observed by BÜTSCHLI (**11**). He interpreted the process as the result of the higher surface tension at the equator of the cell caused by the flow of the protoplasmic currents toward the centrosome. MCCLENDON (**61, 62, 63**), SPECK (**83, 84**), and CHAMBERS (**14**) corroborate BÜTSCHLI's theory by their own observations, and present strong evidence in support of it. KITE (**55**), however, maintains that cleavage is due to "concomitant shrinkage and swelling or change in water-holding power of the different portions of the cytoplasm." GRAY (**49**) thinks that the cleavage furrow is due to an equilibrium established between the effect of the movement in the protoplasm and the surface tension on the surface of the cell. CASTETTER (**12**) agrees with BÜTSCHLI's theory and its supporters.

The division of the protoplasm to form the pollen grains in *O. pratincola* is a process of segmentation through cleavage furrows. Careful observation shows that the granular cytoplasm moves toward the nuclei from the regions of the protoplasm equidistant from the nuclei. This results in vacuolate hyaline regions between the nuclei. The smaller vacuoles fuse to form larger ones arranged between the nuclei. The cleavage furrows progress from the periphery very rapidly, meeting the vacuoles with which they fuse. The process of cleavage is greatly assisted by the presence of the vacuoles with which the furrows fuse as they progress inward.

## Genetical discussion

In many species of *Oenothera* chromosomes do not pair at diakinesis; such is the case in *Oenothera pratincola*. The failure of chromosomes to pair in this genus is presumably due to lack of the

usual affinity resulting from differences in their genetic constitutions. Many explanations have been offered to account for this unusual phenomenon. According to CLELAND (18), chromosomes which pair in diakinesis are relatively homozygous and those which do not are relatively heterozygous. CLELAND (15, 16, 18) suggests that the chain formation is probably due to hybridity. HÅKANSSON (52), in his paper on *Godetia*, states that hybrids present at diakinesis a strong tendency to form circles. On the other hand, GATES (47) finds a regular pairing of the chromosomes in a hybrid of *Oenothera*. OEHLKERS (68) finds in *Oenothera* that there are hybrids with regular pairings as well as those with chains; hence the hypothesis that the formation of rings in certain species of *Oenothera* is an indication of their hybridity, seems untenable. CLELAND (18) also suggests two other ways in which the incompatibility of the chromosomes might have arisen. The first is that it may be due to gradual accumulation of gene mutations within a chromosome. This process, he thinks, is probably aided by the appearance of balanced lethal factors. The second is that, when the chromosomes are arranged end to end, it may be more difficult for them to pair than it is when the homologous chromosomes are placed side by side.

In explanation of the genetical phenomena which *Oenothera pratincola* exhibits, a hypothesis was formulated by BARTLETT (6) which assumes that two unlike types of gametes are produced, which he calls $\alpha$ and $\beta$. Generally the functional egg is an $\alpha$ gamete, and the functional sperm a $\beta$ gamete, the $\beta$ eggs and $\alpha$ sperms usually failing to function. When a zygote is formed in *O. pratincola*, therefore, it generally has the constitution $\alpha\beta$. It receives the $\alpha$ determiners of the female parent and the $\beta$ determiners of the male parent. The results of intercrosses between the entire group of forms indicate that the differences in the characteristics of the several types are in general determined by the $\alpha$ gamete, and thus the modifications of the $\alpha$ gamete are responsible for the greater number of mutations in *Oenothera pratincola*. This is shown by the matroclinic inheritance which the mutations under discussion display in crosses with their parent form. In general, pollination by the $\beta$ gamete of a mutation has the same effect as by a $\beta$ gamete of f. *typica* from which the mutation arose. There are very few characters

that are affected by different sources of the $\beta$ gamete. Among the mutations that have been genetically studied, probably there is no mutation of $\alpha\beta$ constitution effected by a change in the $\beta$ gamete alone except the one reported by DE VRIES (**91**) in the case of *O. biennis sulfurea*. This mutation shows patroclinic inheritance in crosses with its parent.

According to BARTLETT'S hypothesis, the characteristic portion of the $\alpha$ and the $\beta$ gametes may consist of a single chromosome or a group of chromosomes. The chromosomes of the $\alpha$ and the $\beta$ groups do not segregate according to the law of chance in reduction division; instead they pass together as groups to the opposite poles. They are passed to the daughter nuclei as distinct sets, one from the maternal and the other from the paternal parent. In addition to the characteristic chromosome or chromosomes, there may be in some forms chromosomes which are freely segregating. These carry factors for characteristics which show Mendelian inheritance.

For the better understanding of the discussion that is to follow, it is rather important to understand thoroughly what is meant by homologous chromosomes. In most plants and animals, and some of the species of *Oenothera*, when the chromosomes pair during diakinesis, and probably carry allelomorphic factors, such chromosomes are referred to as homologous. In cases when the chromosomes do not pair, and are not known to carry allelomorphic factors, the use of the term homologous chromosomes is rather confusing, because of our present day conception of the term in connection with Mendelism. Some of the chromosomes of *O. pratincola* are not homologous.

When different strains of *Oenothera pratincola* are intercrossed they show a behavior which is very significant genetically. Mut. *formosa* (revolute leaves) is given by strain E (flat leaves). In crosses between the two forms the inheritance is matroclinic, as shown by BARTLETT (**6**) and COBB and BARTLETT (**20**). This behavior of mut. *formosa* shows that it arose from strain E through a change in the $\alpha$ gamete of E. When f. *typica* of strain C is pollinated by mut. *formosa*, the $F_1$ progeny consists of plants in appearance exactly like f. *typica*. All the $F_2$ plants resemble f. *typica*. If mut. *formosa* is used as the pistillate parent and f. *typica* of strain C as the staminate

parent, all the $F_1$ individuals are flat-leaved, resembling strain C. When these $F_1$ individuals are self-pollinated, they give in the $F_2$ generation a ratio of three flat-leaved plants to one having revolute leaves. This simple Mendelian segregation continues in the following generations, as shown by COBB (21). The flat-leaved hybrid strains from this cross (mut. *formosa* × f. *typica* strain C) have been designated as *O. pratincola* strain M by BLANCHARD (COBB 21), and one homozygous flat-leaved strain has been carried under that name for the last seven years. A closed chain of fourteen chromosomes is formed in the final prophase stages (diakinesis), both in mut. *formosa* and in strain C. The homozygous dominant strain M, however, shows at this stage a closed chain of twelve chromosomes to which is attached a pair of chromosomes. These two chromosomes are homologous and contain the factors for flat and for revolute leaves. Such a pair of chromosomes should be expected, in view of the fact that the cross mut. *formosa* × f. *typica* strain C mendelizes and gives a monohybrid ratio in the $F_2$ generation.

As has already been discussed, certain irregularities occur during the heterotypic metaphase, through the deviation of the chromosomes from the characteristic zigzag arrangement, which sometimes result in the abnormal distribution of the chromosomes to the two poles, eight chromosomes going to one pole and six to the other instead of seven and seven. In certain cases, even though the number of chromosomes distributed to each of the two poles is normal, the paternal and the maternal set exchange a chromosome or chromosomes. This gives an abnormal result in breeding. The pollen grain with eight chromosomes may possibly function and give rise to fifteen-chromosomed individuals. The pollen grains with six chromosomes probably do not function at all, as no species have been discovered so far with only thirteen chromosomes. These two cases will be omitted entirely from the discussion that is to follow. The complexes that can arise through an irregularity, even though the distribution of the number of chromosomes to the two daughter nuclei is normal, are many and varied, depending on the nature of the irregularity, the point at which it occurred, and its relation to individual chromosomes, etc. These irregularities have been thoroughly discussed by CLELAND (18, 19). He has also calculated the

theoretical expectancies and the genetical results arising therefrom in case of some such complexes.

From the results of her breeding experiments, FRIEDA COBB BLANCHARD has formed a hypothesis of the constitutions of *O. pratincola* and its revolute-leaved mutations. Her paper dealing with this problem will probably precede the present paper in publication. The hypotheses which she offers have been made known to the writer, and he has adopted them in explanation of his cytological findings. Her explanation of the origin of mut. *formosa* is given in the following paragraph.

Let 1, 2, 3, 4, 5, 6, 7 represent the chromosomes of the $\alpha$ gamete of *O. pratincola* strain E and 8, 9, 10, 11, 12, 13, 14 represent the chromosomes of the $\beta$ gamete. Then the zygote formed will have 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14 as its chromosome constitution. This zygote in reduction division will in turn produce $\alpha$ gametes having chromosomes 1, 2, 3, 4, 5, 6, 7 and $\beta$ gametes having 8, 9, 10, 11, 12, 13, 14. Now suppose an irregularity in the reduction division to occur in the production of the eggs, and chromosome 7 of the $\alpha$ gamete to dissociate from the other members of its series and to become interchanged with chromosome 14 of the $\beta$ series, so that chromosome 7 goes to the $\beta$ complex and chromosome 14 to the $\alpha$ complex. In such a case we shall have 1, 2, 3, 4, 5, 6, 14 for the $\alpha$ gamete and 8, 9, 10, 11, 12, 13, 7 for the $\beta$ gamete. (For an explanation of the conception of this type of a mutation see the section entitled "Whole-chromosome crossovers" in BLANCHARD and BARTLETT 8.) If this modified $\alpha$ egg is fertilized by a regular sperm of *O. pratincola* strain E having 8, 9, 10, 11, 12, 13, 14 as its chromosome constitution, the zygote will have the constitution 1, 2, 3, 4, 5, 6, *14*, 8, 9, 10, 11, 12, 13, *14*. There will be a pair of identical chromosomes in this combination. BLANCHARD believes that mut. *formosa* arises by such a whole chromosome cross-over, the chromosome which becomes duplicated being that one of the $\beta$ complex of strain E which carries the recessive factor for revolute leaves. If this assumption is correct, mut. *formosa* might be expected to show a pairing of two of the chromosomes during the final prophase stages (diakinesis). Apparently, however, there is no such free pair, but it is conceivable that a pair of homologous chromosomes might not

be able to break away from the closed chain. Several others of the revolute-leaved mutations of strain E are probably the results of whole chromosome crossing-over of the type just discussed, where one or more chromosomes from one complex exchange their places with chromosomes of the other complex.

Linkage in *Oenothera* has been the subject of some discussion in recent literature. SHULL (**78, 79**) thinks that, except for the *brevistylis* and old gold (**80**) characters, all the known factors of *Oenothera* probably lie in a single chromosome pair. In this pair SHULL believes that he has located nine factors, affecting visible characters, with which two gametic and two zygotic lethals are supposed to be associated. EMERSON (**31**) has shown that the data offered by SHULL in support of this hypothesis have some discrepancies, and that they do not establish the correctness of the hypothesis.

It appears that linkage in *Oenothera* is due to the cohesion of the chromosomes, and their separation in the heterotypic division in such a way that the maternal set goes to one pole and the paternal set to the other pole of the spindle. It is probable that in *O. pratincola* the maternal and paternal members of the chromosome set alternate with each other, and the characteristic zigzag arrangement at the heterotypic metaphase effects their separation; thus the paternal and maternal sets of chromosomes come out as they enter the zygote. Hence in *O. pratincola* the characteristic group of $\alpha$ chromosomes behaves as a single chromosome and is responsible for a group of linked characters. Interchange of a whole chromosome or chromosomes between the $\alpha$ and the $\beta$ complex does occur as a result of an irregularity in the zigzag arrangement of the chromosomes during the heterotypic metaphase. When such an interchange of chromosomes takes place (a "whole chromosome cross-over") it probably gives rise to a mutation. One case of this type has already been discussed.

GATES (**46**) holds that partial linkage and crossing over probably cannot occur in *Oenothera* because of the telosynaptic arrangement of the chromosomes. Due to such an arrangement, the chromosomes cannot twist about one another during the strepsenema stage and exchange chromatin material, as they do in most plants; hence "crossing over" may not always be possible. CLELAND (**18**) observes

the appressed sides in one or more peripheral loops during late stages of second contraction. These, he thinks, have apparently become twisted about each other in a way that might conceivably result in the exchange of chromatin particles. He thinks crossing over of this type is possible. HÅKANSSON (**53**) also thinks that there is a possibility of crossing over occurring in the second contraction. SHULL (**80**) maintains that the genetical evidence of linkage and crossing over is unequivocal in his cultures. He observes new and striking examples of it every season. *O. pratincola*, which has been under cultivation and has furnished material for the genetical researches of BARTLETT and BLANCHARD for the last fifteen years, does not as yet show any crossing over which cannot be explained by whole chromosome crossing over.

## Summary

1. The diploid chromosome number in *Oenothera pratincola* is fourteen. The chromosomes at metaphase of the somatic mitosis are rod-shaped, variously bent, and are formed by the cross segmentation of the spireme.

2. The resting nuclei of the pollen mother cells are characterized by a network of delicate threads. Chromatin granules varying in size are scattered through the chromatic network, but more thickly at the periphery.

3. There is one large nucleolus and some smaller nucleoli. All of these bodies are in intimate contact with the chromatic network, and probably contribute their material to the spireme developed during the heterotypic prophase. An endonucleolus is present and may be observed from synizesis on to the heterotypic metaphase. The nucleolus is believed to be a storage organ for material related to chromatin, which is drawn upon in the development of the spireme during the heterotypic mitosis.

4. The approach of the heterotypic prophase is indicated by occasional parallel arrangements of the chromatic threads, but these are not very conspicuous. A gradual thickening of the threads is brought about by condensation and the movement of chromatic material along the threads. There is no indication of the fusion of two parallel threads at this stage.

5. As the nucleus enters the prophase, the threads attached to the nuclear membrane seem to contract, probably through condensation, and become gathered to form a ball of threads, the synizetic knot.

6. During synizesis many threads disappear, having delivered their chromatin contents to the threads which are to survive. These become prominent and uniform, and a spireme arises as the knot gradually expands. Some parallelisms are also to be noticed during synizesis, but these are certainly due to the irregular contraction and condensation that take place. Conditions indicate that there is no association or fusion of the separated halves of a univalent spireme or of two univalent spiremes to form a bivalent spireme.

7. The open spireme stage results from the gradual expansion of the synizetic knot, and presents threads of almost uniform thickness throughout the spireme. No free ends were observed in the thread system.

8. By the further contraction and condensation of the threads of the open spireme, the stage known as the second contraction is reached. During this stage all the chromatic material is gathered at the center of the nucleus, the threads in the center thickening more rapidly. Loops of the threads are not lost, even during the stage of greatest contraction, but they become much smaller and radiate from the central mass of chromatic material. These loops are uniformly single threads.

9. The loops could be traced throughout all stages of second contraction, and undoubtedly give rise in part to the univalent chromosomes which emerge at the end of the second contraction. The univalent chromosomes are arranged end to end, that is, telosynaptically.

10. At the stage known as diakinesis in most plants and animals, a closed chain of fourteen chromosomes attached end to end is found in *O. pratincola* strain E, which convincingly points to a telosynaptic association. Occasionally the closed chain breaks at some point to form an open chain of fourteen chromosomes.

11. The chain of chromosomes passes to the equatorial region of the spindle, where the spindle fibers become attached in such a way that alternate chromosomes pass to the same pole. There is a characteristic zigzag arrangement of the chromosomes at metaphase.

12. Anaphase is mostly normal, seven chromosomes passing to each pole; but there are about 3 to 7 per cent of exceptions, due to irregularities in the zigzag arrangement of the chromosomes which result in six chromosomes passing to one pole and eight to the other.

13. A lengthwise split of the chromosomes in preparation for the homeotypic mitosis is effected in late telophase of the heterotypic division.

14. During interkinesis the halves of the split chromosomes (daughter chromosomes) are connected in their middle region; but the ends are widely separated so that each pair resembles an X.

15. The homeotypic divisions are regular and occur simultaneously. The two spindles lie sometimes in the same plane and sometimes at right angles to each other.

16. All of the stages of meiosis in the pollen mother cells of *O. pratincola* strain C are identical with those of *O. pratincola* strain E and of its mut. *formosa*.

17. Strain M (*formosa*×strain C) agrees with *O. pratincola* strain E, strain C, and mut. *formosa* in all the stages of meiosis, up to and including second contraction. Following second contraction, in strain M there emerges a closed chain of twelve chromosomes, with a ring of two attached to it. The ring of two chromosomes breaks away from the closed chain of twelve at the heterotypic metaphase, and the two chromosomes of the pair pass to different poles.

18. This pair of chromosomes is significant of the genetic behavior of strain M. The chromosomes are probably homologous and carry the genes for flat leaf and revolute leaf, and their segregation and recombination in the breeding of strain M give the simple Mendelian ratio.

19. The grand-daughter nuclei pass into a resting condition in which the outlines of the chromosomes become lost in the chromatic network. The process is one of expansion and irregular distribution of the chromatin throughout the nucleus.

20. The segmentation of the protoplasm to form the four pollen grains is effected by furrows which start at the periphery of the pollen mother cell (between the four nuclei) and grow inward, cutting through regions of vacuoles as they pass to the center of the cell.

21. The position of the chromosomes in the chain is believed to be fixed, the maternal alternating with the paternal.

22. The failure of the chromosomes to pair in the late prophase of the heterotypic mitosis is probably because of unlike genetical constitution, but the hypothesis that the formation of chains in certain species of *Oenothera* is an indication of their hybridity is believed to be untenable.

23. *O. pratincola* produces two types of gametes, called $\alpha$ and $\beta$. Generally the functional egg is an $\alpha$ gamete and a functional sperm a $\beta$ gamete.

24. Irregularities in chromosome distribution during the heterotypic metaphase result at times in an exchange of chromosomes, so that an $\alpha$ chromosome enters a $\beta$ complex and vice versa, and such interchange of chromosomes is probably the origin of certain mutations. By the theory of FRIEDA COBB BLANCHARD, presented in the genetical discussion, the origin of mut. *formosa* from *O. pratincola* strain E is due to such an interchange of chromosomes.

25. Certain examples of linkage in *Oenothera* are probably due to cohesion of non-homologous chromosomes in groups. Crossing-over has not been observed in *Oenothera pratincola*.

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UNIVERSITY OF MICHIGAN
ANN ARBOR, MICH.

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## LITERATURE CITED

1. ALLEN, C. E., Nuclear divisions in the pollen mother-cells of *Lilium canadense*. Ann. Botany **19**:189–258. 1905.
2. BARTLETT, H. H., Twelve elementary species of *Onagra*. Cybele Columbiana 37–56. 1914.
3. ———, Additional evidence of mutation in *Oenothera*. BOT. GAZ. **59**:61–123. 1915.
4. ———, Mutation *en masse*. Amer. Nat. **49**:129–139. 1915.
5. ———, Mass mutation in *Oenothera pratincola*. BOT. GAZ. **60**:425–456. 1915.

6. ———, The status of mutation theory, with especial reference to *Oenothera*. Amer. Nat. **50**:513–529. 1916.
7. BEER, RUDOLF, On the development of the pollen grain and anther of some Onagraceae. Beih. Bot. Centralbl. **19**:286–313. 1906.
8. BLANCHARD, FRIEDA COBB, and BARTLETT, H. H., The inheritance of red bud color in crosses of *Oenothera pratincola* and related forms. Papers Mich. Acad. Sci. **6**:77–132. 1926.
9. BOEDIJN, K., Die typische und heterotypische Kernteilung der Oenotheren. Zeitschr. Zellen- u. Gewebelehre. **1**:265–277. 1924.
10. ———, Der Zusammenhang zwischen den Chromosomen und Mutationen bei *Oenothera lamarckiana*. Recueil Trav. Bot. Néerland. **22**:173–261. 1925.
11. BÜTSCHLI, C., Studien über die Entwicklungsvorgänge der Eizelle, die Zelltheilung, und die Kongugation der Infusorien. Senckenb. Naturforsch. Ges. 10. 1876.
12. CASTETTER, E. F., Studies on the comparative cytology of the annual and biennial varieties of *Melilotus alba*. Amer. Jour. Bot. **12**:270–286. 1925.
13. ———, Cytological studies in the Cucurbitaceae. I. Microsporogenesis in *Cucurbita maxima*. Amer. Jour. Bot. **13**:1–10. 1926.
14. CHAMBERS, R., Changes in protoplasmic consistency and their relation to cell division. Jour. Gen. Physiol. **2**:49–68. 1919.
15. CLELAND, R. E., The reduction divisions in the pollen mother cells of *Oenothera franciscana*. Amer. Jour. Bot. **9**:391–413. 1922.
16. ———, Meiosis in the pollen mother cells of *Oenothera franciscana sulfurea*. BOT. GAZ. **77**:149–170. 1924.
17. ———, Chromosome behavior during meiosis in the pollen mother cells of certain Oenotheras. Amer. Nat. **59**:475–479. 1925.
18. ———, Meiosis in the pollen mother cells of *Oenothera biennis* and *Oenothera biennis sulfurea*. Genetics **11**:127–162. 1926.
19. ———, Cytological study of meiosis in anthers of *Oenothera muricata*. BOT. GAZ. **82**:55–70. 1926.
20. COBB, FRIEDA, and BARTLETT, H. H., On Mendelian inheritance in crosses between mass-mutating and non-mass-mutating strains of *Oenothera pratincola*. Jour. Washington Acad. Sci. **9**:462–483. 1919.
21. COBB, FRIEDA, A case of Mendelian inheritance complicated by heterogametism and mutation in *Oenothera pratincola*. Genetics **6**:1–42. 1921.
22. DAVIS, B. M., Pollen development of *Oenothera grandiflora*. Ann. Botany **23**:551–571. 1909.
23. ———, The reduction division of *Oenothera biennis*. Ann. Botany **24**:631–651. 1910.
24. ———, A comparison of the reduction divisions of *Oenothera lamarckiana* and *O. gigas*. Ann. Botany **25**:941–974. 1911.
25. ———, Segregation of *Oenothera brevistylis* from the crosses with *O. lamarckiana*. Genetics **3**:501–533. 1918.

26. ———, Malnutrition as a cause of irregularities in the segregation of *Oenothera brevistylis* from crosses with *Oenothera lamarckiana*. Genetics 6:574–586. 1921.
27. ———, The segregation of *Oenothera nanella-brevistylis* from crosses with *nanella* and with *lamarckiana*. Genetics 11:57–72. 1926.
28. DIGBY, L., The somatic, premeiotic, and meiotic nuclear divisions of *Galtonia candicans*. Ann. Botany 24:727–757. 1910.
29. ———, The cytology of *Primula kewensis* and of other related *Primula* hybrids. Ann. Botany 26:357–388. 1912.
30. ———, On the archesporial and meiotic mitoses in *Osmunda*. Ann. Botany 33:135–172. 1919.
31. EMERSON, S. H., Do balanced lethals explain the *Oenothera* problem? Jour. Washington Acad. Sci. 14:277–284. 1924.
32. ———, The absence of chromosome pairing during meiosis in *Oenothera biennis*. Papers Mich. Acad. Sci. 4:111–114. 1924.
33. FARMER, J. B., and MOORE, J. E. S., New investigations in the reduction phenomena of animals and plants. Proc. Roy. Soc. London 72:104–108. 1903.
34. ———, On the meiotic phase (reduction divisions) in animals and plants. Quart. Jour. Micr. Sci. 48:489–557. 1905.
35. FRASER, H. C. I., and SNELL, J., The vegetative divisions in *Vicia faba*. Ann. Botany 25:845–855. 1911.
36. FRASER, H. C. I., The behavior of chromatin in the meiotic divisions of *Vicia faba*. Ann. Botany 28:633–642. 1914.
37. FARR, C. H., Cytokinesis in the pollen-mother-cells of certain dicotyledons. Mem. New York Bot. Gard. 6:253–317. 1916.
38. ———, Cell division by furrowing in *Magnolia*. Amer. Jour. Bot. 5:379–395. 1918.
39. ———, Quadripartition by furrowing in *Sisyrinchium*. Bull. Torr. Bot. Club 49:51–61. 1922.
40. ———, Meiotic cytokinesis of *Nelumbo*. Amer. Jour. Bot. 9:296–306. 1922.
41. FARR, WANDA K., Cell division of the pollen-mother-cell of *Cobaea scandens alba*. Bull. Torr. Bot. Club 47:325–338. 1920.
42. GATES, R. R., Pollen development in hybrids of *Oenothera lata* × *O. lamarckiana* and its relation to mutation. BOT. GAZ. 43:81–115. 1907.
43. ———, A study of the reduction in *Oenothera rubrinervis*. BOT. GAZ. 46:1–34. 1908.
44. ———, On the origin and behavior of *Oenothera rubricalyx*. Jour. Genetics 4:353–360. 1915.
45. ———, On successive duplicate mutations. Biol. Bull. 29:204–220. 1915.
46. ———, Some points on the relation of cytology and genetics. Jour. Heredity 13:75–76. 1922.
47. ———, The trisomic mutations of *Oenothera*. Ann. Botany 37:543–563. 1923.

48. GEERTS, J. M., Beiträge zur Kenntniss der Cytologie und der partiellen Sterilität von *Oenothera lamarckiana*. Recueil Trav. Bot. Néerland. **5**:93–208. 1909.

49. GRAY, J., Surface tension and cell division. Quart. Jour. Micr. Soc. **66**: 235–245. 1922.

50. GRÉGOIRE, V., La réduction numérique et les cinèses de maturation. La Cellule **21**:297–314. 1904.

51. ——, La formation des gémini hétérotypiques dans les végétaux. La Cellule **24**:369–420. 1907.

52. H.ÅKANSSON, A., Zur Zytologie der Gattung *Godetia*. Hereditas **6**:257–274 1925.

53. ——, Über das Verhalten der Chromosomen bei der heterotypischen Teilung Schwedischer *Oenothera lamarckiana* und einiger ihrer Mutanten und Bastarde. Hereditas **8**:255–304. 1927.

54. KIHARA, HITOSHI, Über das Verhalten der "end to end" gebundenen Chromosomen von *Rumex acetosella* und *Oenothera biennis* während der heterotypischen Kernteilung. Beitrag zur Frage der Para-und metasyndese. Jahrb. Wiss. Bot. **68**:429–460. 1927.

55. KITE, G. L., Studies on the physical properties of protoplasm. I. Amer. Jour. Physiol. **32**:146–164. 1913.

56. LARUE, C. D., and BARTLETT, H. H., Matroclinic inheritance in the mutation crosses of *Oenothera reynoldsii*. Amer. Jour. Bot. **4**:119–144. 1917.

57. ——, An analysis of the changes involved in a case of progressive mutation. Genetics **3**:207–224. 1918.

58. LENOIR, M., Les nucléoles pendant la prophase de la cinèse II du sac embryonnaire du *Fritillaria imperialis*. Compt. Rend. Acad. Sci., Paris **175**: 983. 1922.

59. ——, Sur l'existence de deux variétés de chromatines dans le noyau des cellules des plantes vasculaires. Compt. Rend. Soc. Biol. Paris **88**:771–772. 1923.

60. DE LITARDIÈRE, R., Recherches sur l'élément chromosomique dans la cariocinèse somatique des Filicinées. La Cellule **31**:255–473. 1921.

61. MCCLENDON, J. F., On the dynamics of cell-division. I. The electric charge on colloids in living cells in the root tips of plants. Arch. Entwicklungsmech. **31**:80–90. 1910.

62. ——, On the dynamics of cell division. II. Changes in permeability in developing eggs to electrolytes. Amer. Jour. Physiol. **27**:240–275. 1910.

63. ——, The laws of surface tension and their applicability to living cells and cell-division. Arch. Entwicklungsmech. **37**:233–247. 1913.

64. MICHAELIS, P., Zur Cytologie und Embryoentwicklung von *Epilobium*. Ber. Deutsch. Bot. Ges. **43**:61–67. 1925.

65. MOTTIER, D. M., The development of the heterotype chromosomes in pollen mother-cells. Ann. Botany **21**:309–347. 1907.

66. ———, On the prophases of the heterotypic mitosis in the embryo-sac mother-cell of *Lilium*. Ann. Botany **23**:343–352. 1909.
67. ———, Mitosis in the pollen mother-cells of *Acer negundo* L. and *Staphylea trifolia* L. Ann. Botany **28**:115–133. 1914.
68. OEHLKERS, F., Erblichkeit und Zytologie einiger Kreuzungen mit *Oenothera strigosa*. Jahrb. Wiss. Bot. **65**:401–446. 1926.
69. ROSENBERG, O., Zur Kenntnis der Reduktionsteilung in Pflanzen. Bot. Notiser **1**:1–24. 1905.
70. ———, Zur Kenntnis von den Tetradenteilungen der Compositen. Svensk. Bot. Tidskr. **3**:64–77. 1909.
71. ———, Über den Bau des Ruhekerns. Svensk. Bot. Tidskr. **3**:163–173. 1909.
72. SCHWEMMLE, J., Vergleichend zytologische Untersuchungen an Onagraceen. Ber. Deutsch. Bot. Ges. **42**:238–243. 1924.
73. ———, Vergleichend zytologische Untersuchungen an Onagraceen. II. Die Reduktionsteilung von *Eucharidium concinnum*. Jahrb. Wiss. Bot. 65: 778–818. 1926.
74. ———, Der Bastard *Oenothera berteriana*×*Onagra* (*muricata*) und seine Zytologie. Jahrb. Wiss. Bot. **66**:579–595. 1927.
75. SHARP, L. W., Somatic chromosomes in *Vicia*. La Cellule **29**:297–331. 1913.
76. ———, Somatic chromosomes in *Tradescantia*. Amer. Jour. Bot. **7**:341–354. 1920.
77. SHULL, G. H., A peculiar negative correlation in *Oenothera* hybrids. Jour. Genetics **4**:83–102. 1914.
78. ———, Linkage with lethal factors the solution of *Oenothera* problem. Eugenics, Genetics, Family **1**:86–99. 1923.
79. ———, Further evidence of linkage and crossing over in *Oenothera*. Genetics **8**:154–167. 1923.
80. ———, "Old-gold" flower color, the second case of independent inheritance in *Oenothera*. Genetics **11**:201–234. 1926.
81. SINOTÔ, YOSITO, On the nuclear divisions and partial sterility in *Oenothera lamarckiana* Ser. Bot. Mag. Tokyo **36**:92–98. 1922.
82. ———, Microsporogenesis in *Oenothera sinuata* L. Bot. Mag. Tokyo **41**: 225–234. 1927.
83. SPECK, J., Oberflächenspannungsdifferenzen als eine Ursache der Zellteilung. Arch. Entwicklungsmech. **44**:1–113. 1918.
84. ———, Die amöboiden Bewegungen und Strömungen in den Einzellen einiger Nematoden während der Vereinigung der Vorkerne. Arch. Entwicklungsmech. **44**:217–255. 1918.
85. STOMPS, T. J., Kerndeeling en synapsis bij *Spinacia oleracea*. Biol. Centralbl. **31**:257–320. 1910.
86. TÄCKHOLM, G., Zur Kenntnis der Embryosackentwicklung von *Lopezia coronata*. Svensk Bot. Tidskr. **8**:223–234. 1914.

87. TAMURA, O., Morphologische Studie über Chromosomen und Zellkerne. Arch. Zellf. **17**:131–164. 1923.

88. VALCANOVER, ROBERTO, Contribution à l'étude de la reduction dans l' *Oenothera biennis*. La Cellule **37**:203–222. 1926.

89. VAN CAMP, G. M., Le rôle du nucléole dans la caryocinèse somatique (*Clivia miniata* Reg.). La Cellule **34**:2–48. 1924.

90. DEVRIES, HUGO, Mutationstheorie. 2 vols. Leipsic: Veit & Co. 1901, 1903.

91. ——, Gruppenweise Artbildung. viii+365. Berlin: Gebrüder Borntraeger. 1913.

92. ——, *Oenothera gigas nanella*, a Mendelian mutant. BOT. GAZ. **60**:337–345. 1915.

93. WAGER, H., The nucleolus and the nuclear division in the root-apex of *Phaseolus*. Ann. Botany **18**:29–55. 1904.

## EXPLANATION OF PLATES VII–IX

All figures were sketched with the aid of a camera lucida, under a Spencer microscope, with Spencer 1.8 oil-immersion objective and 18× eye-piece; they have been reduced here one-fourth in reproduction; present magnification approximately 1400 diameters. *Oenothera pratincola* strain E unless otherwise stated.

### *PLATE VII*

FIG. 1.—Metaphase of mitosis in archesporial cell viewed from pole of spindle, showing fourteen chromosomes.

FIG. 2.—Early anaphase of mitosis in archesporial cell.

FIG. 3.—Resting nucleus of pollen mother cell.

FIG. 4.—Gradual thickening of threads, with occasional parallelism, approaching prophase of heterotypic mitosis.

FIG. 5.—Advanced stage in thickening of threads, giving a coarse reticulum.

FIG. 6.—Beginning of contraction of reticulum prior to synizesis; threads varying greatly in thickness.

FIG. 7.—Early synizesis showing irregular thickening of threads.

FIG. 8.—Mid-synizesis.

FIG. 9.—Loosening of synizetic knot; threads somewhat thicker and more uniform.

FIG. 10.—Open spireme emerging from synizesis; note mass of contracted threads at left.

FIG. 11.—Open spireme, single threads.

FIG. 12.—Open spireme, thread showing chromomeres.

FIG. 13.—Second contraction; note thickening of threads in center and peripheral loops.

FIG. 14.—Second contraction, showing thick threads just before differentiation of chromosomes.

FIG. 15.—Second contraction; three chromosomes distinct.

FIG. 16.—Second contraction; chromosomes evident.

*PLATE VIII*

FIG. 17.—End of second contraction stage; chromosomes distinct but still crowded.

FIGS. 18–20.—Closed chains of fourteen chromosomes in late prophase.

FIG. 21.—Open chain of fourteen chromosomes in late prophase due to break in one of attachments.

FIG. 22.—Closed chain of fourteen chromosomes; multipolar spindle omitted.

FIG. 23.—Open chain of fourteen chromosomes; multipolar spindle.

FIG. 24.—Heterotypic metaphase showing regular zigzag arrangement of chromosomes; alternate chromosomes go to same pole.

FIG. 25.—Two chromosomes (*a*, *b*) in different parts of chain suspended between the poles.

FIG. 26.—Two pairs of adjacent chromosomes (*a*, *b*) passing to different poles of spindle.

FIG. 27.—Pair of adjacent chromosomes (*a*) passing to one pole with single chromosome (*b*) suspended on equatorial plate.

FIGS. 28–30.—Chromosome groups with fiber attachments so irregular that distribution of chromosomes is uncertain.

FIG. 31.—Late anaphase, polar views.

Fig. 32.—Late anaphase, showing unequal distribution of chromosomes (6 and 8).

*PLATE IX*

Fig. 33.—Late anaphase, polar view, showing typical arrangement of chromosomes.

FIG. 34.—Interkinesis, showing split chromosomes and formation of new nucleoli.

FIG. 35.—Interkinesis, showing X-like pairs of daughter chromosomes with denser regions.

FIG. 36.—Homeotypic prophase with pairs of daughter chromosomes now condensed; an example of irregular distribution, six chromosomes in one nucleus and eight in other; note prominent split in chromosomes.

FIG. 37.—Homeotypic metaphase; side view of one plate and polar view of other, showing regular distribution of chromosomes.

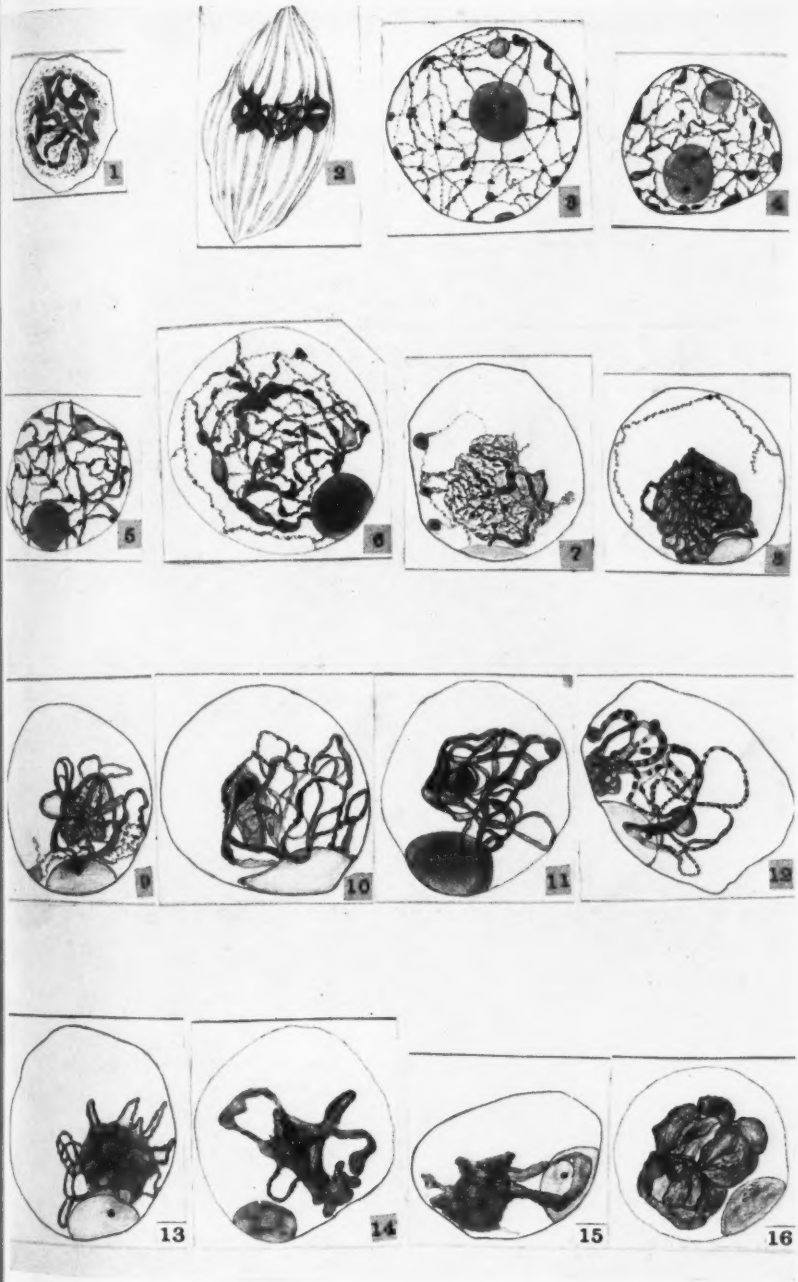
FIG. 38.—Telophase of homeotypic mitosis, chromosomes spun out into threads forming irregular network.

FIG. 39.—Closed chain of fourteen chromosomes in mut. *formosa;* late prophase.

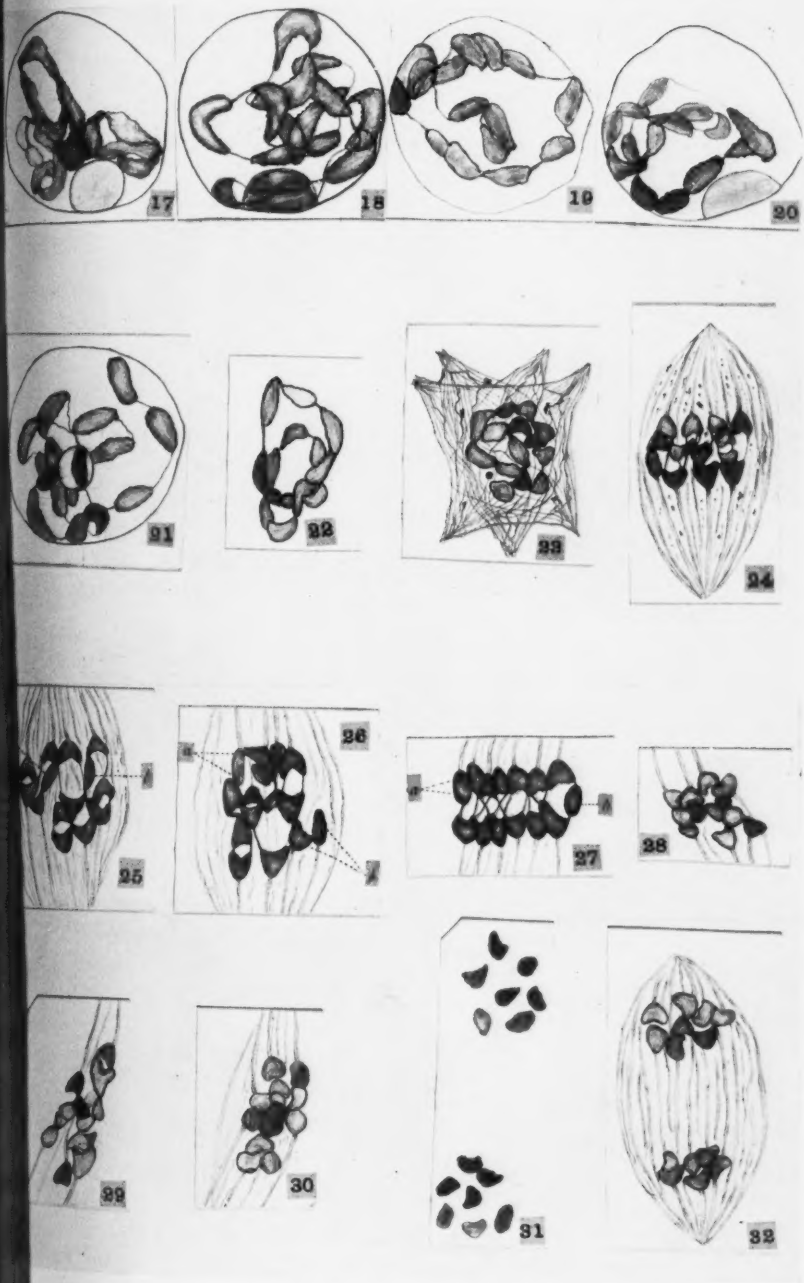
FIG. 40.—Open chain of fourteen chromosomes in mut. *formosa*, result of break in chain; late prophase.

FIG. 41.—Closed chain of twelve chromosomes and ring of two (*a*) in strain M; late prophase.

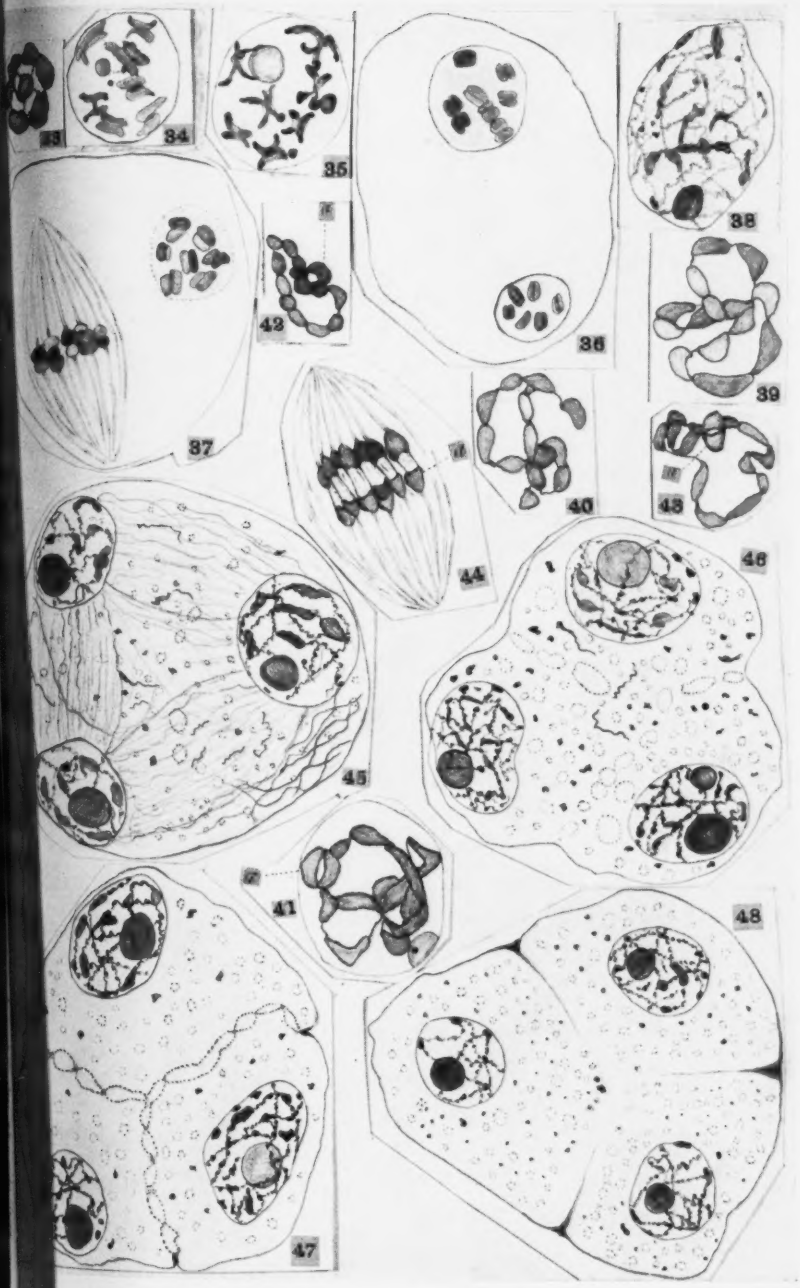
FIG. 42.—Closed chain of twelve chromosomes and ring of two (*a*) in strain M; multipolar spindle omitted.




KULKARNI on OENOTHERA




KULKARNI on OENOTHERA




KULKARNI on OENOTHERA

FIG. 43.—Same as fig. 42.

FIG. 44.—Metaphase of heterotypic mitosis in strain M; chain of twelve chromosomes and ring of two (*a*) at side of spindle separate from chain.

FIG. 45.—Late telophase of homeotypic mitosis; boundaries of some of chromosomes still visible; note spindle fibers connecting nuclei.

FIG. 46.—Late telophase; small refractive vacuoles in cytoplasm; wall of pollen mother cell infolded between nuclei.

FIG. 47.—Large flattened vacuoles formed by fusion of vacuoles between nuclei from center of pollen mother cell to furrows at periphery.

FIG. 48.—Furrows cutting inward from periphery toward center of pollen mother cell.

# A REVISION OF THE GENUS COLLINSIA (SCROPHULARIACEAE)

VESTA MARIE NEWSOM

## Introduction

In 1924, ALICE MCCULLY MUNZ undertook a study of the southern California species of *Collinsia*. From her work it soon became evident that the genus as a whole needed revising, the most recent complete treatment being that of GRAY (Syn. Fl. N. Am. 2:255–257, supplement 439, 1886). The next year DR. PHILIP A. MUNZ of Pomona College, while working in the library of the Gray Herbarium, got together notes and copied species descriptions for the group as a whole. It was at his suggestion and under his direction that, in the fall of 1925, the present paper was undertaken.

In addition to expressing appreciation to Dr. MUNZ for his help and direction, I wish to acknowledge with gratitude the loan of material and supplying of information by the following: Dr. B. L. ROBINSON and Dr. IVAN M. JOHNSTON of the Gray Herbarium, Dr. W. L. JEPSON of the University of California, Dr. F. W. PENNELL of the Philadelphia Academy of Natural Sciences, Dr. L. R. ABRAMS of Stanford University, and Dr. HAROLD ST. JOHN of the State College of Washington. To Mrs. ALICE MCCULLY MUNZ and Mr. DAVID D. KECK I express my thanks for field color notes of several species.

In citing herbarium material the following symbols are used: Gray Herbarium of Harvard University (G), Dudley Herbarium of Stanford University (S), Jepson Herbarium (J), Pomona College Herbarium (P).

## History of treatment of genus

The genus *Collinsia* was first described by NUTTALL (Jour. Acad. Philad. 1:190. *t.* 9. 1817). He had collected *Collinsia verna*, the type species, as early as 1810 along the Allegheny River and Lake Erie, but the specimens were lost. In 1816 he again found it in seed at Gallipolis, Ohio, and based his generic and specific descriptions on

the plants raised from the seeds collected. The genus was dedicated to ZACCHEUS COLLINS of Philadelphia, who was a "very worthy botanist," but published nothing. RAFINESQUE (Am. Mo. Mag. 4: 194. 1819; Cincin. Lit. Gaz., 84. 1824) stated that Dr. MILLER of Pennsylvania was the first to find *Collinsia*, but that MUHLENBERG in classifying it mistook it for a new species of *Herpestis*. In the latter publication RAFINESQUE adds two new species, makes eight new varieties, and later (Cat. 13) adds a fourth species. DOUGLAS (LINDL., Bot. Reg. *t.* 1082 and *t.* 1107. 1827) was the first to publish far-western species, naming *C. parviflora* and *C. grandiflora* respectively. He sent seeds of another western species to BENTHAM, who grew them and then described *C. bicolor* (Trans. Hort. Soc. n. ser. 1:480. 1834). About this time, NUTTALL published two more species, *C. minima* (Jour. Acad. Philad. 7:47. 1834) and *C. violacea* (Trans. Am. Phil. Soc. 5:179. 1837). FISCHER and MEYER (Ind. Sem. Hort. Petrop. 2:33. 1836) named *C. sparsiflora*, and R. GRAHAM *C. heterophylla* (HOOK., Bot. Mag. *t.* 3695. 1838). WALPERS (Repert. 3:231–2. 1844–45) was the first to list the known species, and BENTHAM (DC., Prod. 10:318–19, 593. 1846) made the first comprehensive study of what was then a comparatively small genus. He added two new species.

New discoveries were made from time to time, but no further study of the group as a whole was made until ASA GRAY worked over the California species then known (Bot. Calif. 1:552–555. 1876), and later published the last complete treatment of the genus (Syn. Fl. N. Am. 2:255–57, supplement 439. 1886). Since then there have been many treatments in manuals covering restricted areas, and several new species and varieties have been added. The only recent study that is of real importance, however, is that made by JEPSON (Man. Calif. 902–905. 1925), which is a treatment of Californian plants only.

There has been a total number of forty-seven species published for the genus, and of this number seventeen species and twelve varieties are being recognized in this paper.

The genus *Collinsia* is very distinctly a unit, although it has on occasion been confused with *Tonella* (BENTH., in DC., Prod. 10:593. 1846; GREENE, Pittonia 1:55. 1887), but the presence of the keel-

shaped middle lobe of the lower lip in *Collinsia* readily separates the two. Aside from *Tonella*, *Collinsia* seems to have no other close relatives.

There is little evidence of specialization within the genus, except with reference to seed characters, which are discussed later. Generally speaking, the species all seem to be at about the same level of development, none being particularly primitive or specialized. However, they can quite easily be arranged in series. The length of the pedicels forms the basis for the most conspicuous division of the genus into the sessile- and pedicel-flowered groups, and these in turn are easily arranged in series according to bearding of stamen filaments or size and shape of corollas. ASA GRAY was the first to use the character of long and short pedicels in keying the species, and it has been used for the main grouping in all subsequent studies.

As to geographical distribution, all except two species occur in California, but they are not all restricted to this state. Only three species occur east of the Rocky Mountains. The sessile-flowered species are restricted to California and Lower California, while the pediceled ones range from east to west coast and from Lower California into Canada. *C. parviflora* is the most widely distributed species, occurring from the Rocky Mountains westward to the coast and from Canada to southern California, and eastward to Lake Superior.

### Diagnostic characters for species

In searching for workable units, such gross characters as leaf size and shape, calyx shape, and the pubescence of the whole plant all have been found variable within a given species and thus not of much importance in a taxonomic study. With the exception of the long- and short-pediceled character, all the most important specific characters refer to the corolla, the stamens, and the seeds.

Corolla size may or may not be variable. In the *torreyi* group it is very constant in each variety, while in the *sparsiflora* group numerous intergradations, both in size and in shape of corolla, make the series a difficult one with which to work. In the large-flowered sessile forms variation in the length of the upper lip is a constant and workable character.

Variation in corolla color I am entirely disregarding, because

if such were considered, innumerable varieties would have to be made. For instance, *C. bicolor* var. *typica* has every intermediate shade between white or pale pink to very deep violet-blue. In *C. bartsiaefolia* var. *typica* there is intergradation from white to rose-lavender. These are closely allied shades, and when not consistent in variation do not seem worthy of taxonomic recognition. The revision must be based on more fundamental and constant structural characters.

Bearding on the lower half of filaments (usually on just the upper pair), although not always easily discernible, is most helpful in making some rather large and important groupings in comparison with species with glabrous stamen-filaments.

The size and shape of the seeds are important in numerous cases. There are two extremes in seed development. Species which have flattened and often winged or cup-shaped seeds when mature are found in all the sessile-flowered group, and in *sparsiflora*, *rattanii*, and *franciscana* of the long-pediceled group. Those seeds which become thickened and bean-shaped when mature characterize all the long-pediceled forms except those just mentioned. The seeds of the *rattanii* group and of *franciscana* really indicate an intermediate position between the two groups, however, generally not being thickened enough to belong to the second group, and yet not thin-margined enough for the first. The thickened seed is evidently the most highly developed, because the seeds of all the species are at least somewhat flattened when immature. If it were not for the intermediate groups, this seed character would offer a very good means of sub-generic division, but I do not feel that it is definite enough.

### Description of genus

COLLINSIA.—Jour. Acad. Philad. 1:190, *t.* 9. 1817; Rafin., Cincin. Lit. Gaz. (for Neophyton 2), 84. 1824; Endl. Genera Pl., 3897. 1840; Benth., in DC. Prod. 10:317. 1846; Benth. & Hook. Genera Pl. $2^{11}$:941. 1876; Gray Syn. Fl. N. Am. 2:246, 255. 1878; Baillon Hist. de Pl. 9:436. 1888; Gray Man., ed. II: 380. 1889; Engler-Prantl Pflan. Fam. 4, III*b*:64. 1895; Howell Fl. N.W. Am. 1:505. 1901; Britton & Brown Fl. N. U.S. & Can. ed. II, 3:188. 1913; Jepson Man. Calif., 901. 1925.

Annual herbs, 5–50 cm. tall, erect, decumbent or loosely branched, glabrous to puberulent or glandular-pubescent. Leaves opposite or whorled, petioled below to sessile above, entire or occasionally three- to five-parted below. Pedicels bracteate to ebracteate, short and almost sessile to long and filiform, one-flowered. Flowers in two- to eight-flowered whorls, forming a raceme with each whorl, cymose with pedicels not evident, or solitary and axillary. Calyx of five united sepals, campanulate, cleft; lobes subequal, the two lower ones broader and slightly shorter, the uppermost somewhat folded and appressed to the tube when tube is saccate. Corolla of five united petals, two-lipped, papilionaceous; corolla-tube straight or recurved, tubular to gibbous or saccate near base dorsally; upper lip two-lobed, with a transverse ridge or two-crested region within from which the lip is reflexed; lower lip three-lobed, the lateral lobes spreading-pendulous, middle lobe conduplicate into a keel-shaped sac which incloses the four declined stamens and style; keel coalesced one-half to one-third its length with lateral lobes to form an inconspicuous infolding saccate region descending into the tube as far as the lip divisions. Filaments four, didynamous, long and filiform, the lower or anterior pair inserted higher on the tube than the upper pair and somewhat shorter. Anthers roundreniform, the two cells confluent at the apex into one, 0.5–1 mm. wide, closely infolded with the stigma near the tip of the keel (or rarely exceeding the keel in old corollas). Rudimentary stamen or gland conical to oblong, located at the base of the corolla tube dorsally. Style long and filiform, persistent. Stigma small, capitate-entire to two-cleft. Capsule ovate or globose, glabrous, or rarely slightly pubescent, septicidal; valves two-cleft. Seeds amphitropous, peltate, dorsally convex, concave ventrally, flattened and winged to rounded and not winged, smooth to reticulate, two to many.

Type species for genus: *C. verna* Nutt.

### Key to species

A. Flowers sessile, congested in whorls, with pedicels shorter than (to no longer than) the calyces in the lower whorls; seeds flattened when mature.

B. Upper pair of filaments with no basal appendage, or with a rudimentary one present less than 1 mm. long.

C. Upper lip of corolla conspicuously shorter than lower, or its sinus not over 2 (3) mm. deep.

D. Filaments (at least the upper ones) well bearded; upper corolla lip with transverse but no conspicuous lateral callous crests at throat; pedicels of whorls shorter than calyces.

E. Dorsal region of tube saccate, conspicuous, 3–4 mm. deep, short gland-bearded within; lateral corolla lobes usually long-bearded subcentrally, and longer and wider than keel; seeds 4, 2–3 mm. long; keel 1–2 mm. shorter than lateral lobes; leaves triangular-lanceolate, usually over 4 cm. long.....1. *C. tinctoria*

E. Dorsal region of tube gibbous, inconspicuous, ca. 1 mm. deep, long-bearded within; lateral corolla lobes not bearded subcentrally, and equaling the keel in size; seeds more than 4, 1–1.5 mm. long; keel as long as lateral lobes; leaves oblong, crenate, not over 3 cm. long.

F. Flowers over 13 mm. long, in dense capitate clusters or whorls; plant rather stout, branching, diffuse, almost decumbent (occasionally erect); veining of corolla lobes not conspicuous. Mendocino County to vicinity of San Francisco, California. 2. *C. corymbosa*

F. Flowers less than 10 mm. long, in several slender whorls; plant slender, erect; veining of corolla lobes evident. Monterey and San Benito Counties and Sierran California.....3. *C. bartsiaefolia*

D. Filaments glabrous, the upper pair bearded at base; upper corolla lip with distinct lateral and transverse callous crests projecting into throat; pedicels of lower whorls as long as calyces.....6. *C. greenei*

C. Upper lip of corolla as long as or slightly shorter than lower lip, its sinus more than 2 mm. deep; plants erect.

D. Leaves thin, serrulate-entire; corolla lavender-blue, appearing truncate, veining of lobes not evident. Foothills of San Bernardino Mts. south to Lower California

4. *C. concolor*

D. Leaves thick, crenate; corolla white to rose-lavender, lobes broad and rounded, veins evident and usually somewhat darkened . . . . . 3. *C. bartsiaefolia*

B. Upper filaments with a distinct basal appendage 1–2 mm. long . . . . . 5. *C. bicolor*

A. Flowers pediceled, solitary or in whorls; pedicels of lower corollas from as long as to longer than calyces; seeds thickened or flattened.

B. Upper filaments bearded (occasionally very sparsely so in 10e and 11).

C. Plants from east of Rocky Mountains (corolla over 8 mm. long).

D. Seeds normally 4, 2–3 mm. long; upper lip of corolla white or tinged lavender, almost equaling lower lip in length; lower lip bright blue; corolla lobes retuse; calyx rather pale, submembranous below; leaves thin, ovate to deltoid-lanceolate. New York to Missouri . . . . . 8. *C. verna*

D. Seeds 6–12, 1–1.5 mm. long; corolla bright violet, upper lip slightly paler and conspicuously shorter than lower lip; corolla lobes obcordate, notch acute, 1 mm. deep; calyx purplish, inconspicuously submembranous below; leaves thickened, oblong to lance-oblong. Southeastern Kansas, southwestern Missouri to Texas . . 9. *C. violacea*

C. Plants from west of Rocky Mountains (corolla 4–6 mm. long, except in no. 12).

D. Plants from central California and northward; mature seeds thin and flattened, winged, 2–3 mm. long.

E. Inflorescence glandular-pubescent, often viscid; cauline leaves deltoid-ovate to lance-ovate; corolla 12–18 mm. long; upper lip white, lower bluish-purple. San Francisco, San Mateo, Santa Clara counties . . . . . 7. *C. franciscana*

E. Inflorescence glabrous to sparse-pubescent; cauline leaves oblong to lanceolate; corolla whitish-lavender to purple . . . . . 10. *C. sparsiflora*

D. Plants of southern California; mature seeds thick, not winged, 1 mm. long; upper stem and pedicels finely retrorse-pubescent . . . . . 11. *C. parryi*

B. Upper filaments glabrous, except for some bearding at place of attachment.

C. Bracts at least 2 mm. long in upper whorls of inflorescence (in number 15, the uppermost bracts may be shorter).

D. Upper lip of corolla with no conspicuous lateral and transverse callous crests projecting into throat.

E. Dorsal side of tube saccate when corolla is over 7 mm. long, or at least gibbous when corolla is less than 7 mm. long; corolla throat closed by the declined callous ridge of upper lip; calyx lobes subulate-acuminate; inflorescence glabrate to pubescent or inconspicuously glandular-pubescent; seeds 4.

F. Corolla 4–6 mm. long, white and blue to violet-blue; corolla tube gibbous at base, erect or slightly declined; corolla lips inconspicuously divergent, $\frac{1}{3}$ the total corolla length, lobes narrowed and entire; calyx over half the length of corolla, its lobes somewhat concealing the corolla tube.....12. *C. parviflora*

F. Corolla over 6.5 mm. long, violet; corolla tube deeply saccate at base, strongly declined to form a right angle with pedicel; corolla lips divergent, $\frac{1}{2}$–$\frac{1}{3}$ the corolla length, lobes broad in appearance, retuse or emarginate; calyx $\frac{1}{3}$–$\frac{1}{2}$ the corolla length, its lobes not concealing the corolla tube.....13. *C. grandiflora*

E. Dorsal side of tube merely gibbous when corolla is over 7 mm. long, tubular when corolla is less than 7 mm. long; corolla throat open, callous ridge not declined into the throat; calyx lobes linear to subulate (acuminate), obtuse to rather broadly acute; inflorescence conspicuously glandular-(viscid-) pubescent (no. 16 variable).

F. Cauline leaves linear, thickened, gray-green. Northern California to Washington.....14. *C. rattanii*

F. Cauline leaves ovate to oblong. Southern and central California.

G. Seeds 2, ca. 3 mm. long; leaves thin; calyx membranous, rounded and ca. 3 mm. wide at base in fruit, lobes exceeding the capsule....15. *C. childii*

G. Seeds 6–8, ca. 2 mm. long; calyx and leaves thick and succulent; calyx squared and swollen, ca. 5 mm. wide at base in fruit, lobes about equaling the length of the capsule.....16. *C. callosa*

D. Upper corolla lip with conspicuous lateral and transverse callous crests projecting into throat. North coast ranges, California .....6. *C. greenei*

C. Bracts of inflorescence obsolete, or minute and less than 2 mm. long in upper whorls (leafy bracts ca. 1 cm. long when plants are immature or 1–2 flowered, otherwise typical); corolla throat open; seeds 2; calyx never membranous below, lobes not longer than the mature capsule....17. *C. torreyi*

**Treatment of species**

1. COLLINSIA TINCTORIA Hartw., in Benth. Pl. Hartw., 328. 1848; Gray Syn. Fl. No. Am. **2**:255. 1878; Jepson Man. Calif., 902. 1925; *C. barbata* Bosse, Verh. Berl. Gartenb. Ver. N. Reihe **1**:399. 1853; *C. septemnervia* Kellogg, Proc. Cal. Acad. **2**:224. 1863.

Plant 20–60 cm. high; stems simple, erect, or occasionally sparsely branched, glabrous below, glandular-viscid above, imparting a brownish stain; leaves thin, ovate to broadly triangular-lanceolate, acute, serrate-crenate to entire, scabrous, sessile by a broad or subcordate base, glabrous to sparsely puberulent above, puberulent below, 1–10 cm. long, 0.5–4.0 cm. wide; lower leaves oblong, obtuse, with petioles 5–10 mm. long; flowers in 2–6 many-flowered whorls, sessile or with pedicels not over 2 mm. long; bracts linear, entire, glandular-pubescent, 5–10 mm. long, ca. 1 mm. wide; calyx deeply parted, submembranous at base, 5–8 mm. long; calyx lobes linear to lanceolate, obtuse to broadly acute, densely glandular-pubescent, 4–7 mm. long, ca. 1 mm. wide; corolla strongly declined, yellow to greenish white, with purple dots or lines, 12–16 mm. long; corolla tube 5 mm. long, ca. 2 mm. wide at base, abruptly widened by the dorsal saccate region; saccate region short gland-bearded within, 3–4 mm. deep at base, forming a right or obtuse angle with the tube; upper lip 4–5 mm. long, ca. 2 mm. of the lip length reflexed from the transverse calloused ridge; lobes rudimentary, emarginate, sinus less than 1 mm. deep; lower lip 5–10 mm.

long, keel 1–2 mm. shorter than the lateral lobes; lateral lobes ovate-spatulate, obtuse, entire, long-bearded within at subcentral region, 4–5 mm. wide; keel sparsely gland-bearded without, 2–3 mm. deep; lateral inverted saccate region sparsely gland-bearded within; upper pair of filaments bearded half their length; rudimentary basal appendage not over 0.8 mm. long, bearded; lower filaments rarely bearded; anthers brick red; stigma not lobed; capsule 3–4 mm. long, well exceeded by calyx lobes; seeds flattened, round-oblong, rugose-reticulate without, smoother within, slightly winged, 2–3 mm. long, 1–2 mm. wide, normally 4 in number.

**Type locality.**—"In montibus Sacramento."

**Representative material.**—CALIFORNIA: without locality, *Hartweg* 1882, in 1846–47, type collection (G); between McCloud and Sacramento rivers, *Heller* 12498 (S); Table Mountain, 8 miles north of Oroville, *Heller* 10768 (S); Little Chico, *Bruce* 1845 (P); Mt. Diablo, North Peak, *Jepson* 7612 (S), on road to summit, *Abrams* 8019 (S); Sonoma Creek at the foot of Mt. Hood, *Heller* in 1902 (S); Eshom Valley, *Clemens* in 1910 (P); vicinity of Homer's Nose, Sequoia National Park, *Dudley* 1811 (S); South Fork of Kings River, *Clemens* in 1910 (P); Collins Meadow, *Hall & Chandler* 459 (P, S); Yosemite Valley, Kenneyville, *Abrams* 4554 (S); Yosemite Valley, *M. E. Jones* in 1884 (P); the trail from Tioga Road to Yosemite Falls, *Munz* 7518 (P); Mather, *Munz* 7367 (P); Longworthy's near North Fork, Sierra National Forest, *Abrams* 4966a (S); Big Trees, Calaveras Co., *Dudley* in 1906 (S); Kelsey, El Dorado Co., *M. E. Jones* in 1883 (P).

This species, while it has considerable variation in the amount of pubescence and in leaf length, is constant as to corolla and seed characters. Plants from two localities are exceptions to the description given for the species, but do not seem to justify varietal rank. Material cited from Mt. Diablo, while typical in floral structure, has thickened and rather succulent leaves, due probably to ecological conditions. It is also often dwarfed in growth, for example, *Jepson* 7612 (S) is only 10 cm. high. *Munz* 7518 from the Tioga trail to Yosemite Falls (P) is peculiar in that the lateral lobes have no subcentral bearding; the lobes of the upper lip are rather larger and more conspicuous than ordinary, and the dorsal saccate region is less conspicuous than in typical material.

2. COLLINSIA CORYMBOSA Herder, Ind. Sem. Hort. Petrop., 32. 1857; Regel, Gartenfl. **33**: *t.* 568. 1868; Gray Syn. Fl. No. Am. **2**:

255. 1878; Jepson Man. Calif., 903. 1925; *C. bartsiaefolia* of Jepson, *l.c.*, in part.

Diffusely branched, almost decumbent, occasionally simple and erect; branches finely white-pubescent to glabrate, infrequently sparsely glandular, 10–18 cm. long; leaves rather fleshy, oblong to ovate or elliptical, obtuse, crenate, villous to glabrate above, glabrous below, 10–20 mm. long, 5–10 mm. wide; flowers sessile or with pedicels not over 5 mm. long, in whorls of 3 to 10, these either crowded in a terminal inflorescence, appearing corymbose, or 1 cm. or more apart; bracts crenulate, sparsely to densely villous-pubescent, 5–9 mm. long, 3–5 mm. wide; calyx puberulent to conspicuously villous-pubescent, "whitish green," 7–10 mm. long; calyx lobes oblong to broadly ovate, obtuse, 3–5 mm. long, 1.5–2 mm. wide; corolla strongly declined, pale lavender to yellowish-white, long and appearing tubular, the outspread lobes not over half the total corolla length, 13–20 mm. long; corolla tube 7–10 mm. long, 3–5 mm. wide; dorsal gibbous region of tube shallow, 1 mm. deep, bearded within, the bearding becoming longer toward the top; upper lip blue, 3–7 mm. long, the lobes yellowish, reflexed, from apiculate and almost obsolete to truncate and 4–6 mm. long; the sinus 1–2 mm. deep; lower lip 10–20 mm. long; lateral lobes as long as the keel, entire or retuse, broadly spatulate, 4–6 mm. wide, somewhat divergent; keel 3–5 mm. deep; upper pair of filaments bearded for half their length; lower filaments more sparsely bearded; stigma not lobed; capsule 5–6 mm. long, exceeded by the calyx lobes; seeds flattened, oblong, many, irregularly winged, finely rugose-reticulate, 1–1.5 mm. long.

**Type locality.**—"from Mexico" according to Regel, *l.c.*, but this is certainly incorrect, since the range is restricted to the north-central coast of California.

**Material studied.**—CALIFORNIA: without locality, *Samuels* (G), *Dr. Gibbons* in 1853 (G), *Kellogg & Harford* 660 (G); Ft. Bragg, *Bolander* 4783 (G); Bolenas Bay, *Bigelow* in 1849 (G); San Francisco, *Jones* in 1882 (P), *Greene* 161 (G); Mt. Lake, San Francisco, *Eastwood* in 1894 (G); Lake Merced, S.F. Co., *Abrams* 1601 (S); Presidio, S.F., *Dudley* in 1902 (S), *Baker* 710 (P), *Michener & Bioletti* 77 (G), *Tidestrom* in 1895 (P).

This species is amply distinct from *C. bartsiaefolia* var. *typica*, with which it has been confused, in having a shorter upper lip, corolla lobes not evidently veined, and the corolla appearing tubular. Typical *corymbosa* has a very short apiculate upper lip (for example,

*Bolander* 4783 and *Baker* 710), but this character is variable, and in material from the same locality as the *Baker* collection are found all intergradations from apiculate lobes ca. 1 mm. long to truncate lobes, with a sinus between them ca. 2 mm. deep (*Jones* in 1882). Because of the scarcity of material and the limited range, it is thought best not to make a separate variety of the form with the longer upper lip.

3. COLLINSIA BARTSIAEFOLIA Benth. in DC. Prodr. **10**:318. 1846.

Stems erect, or diffusely branching, puberulent below, villous and often glandular above, 10–35 cm. long; leaves somewhat erect, oblong to lance-oblong, obtuse, crenate, rarely entire, scabrous-margined, thickened, sparsely villous, 1–4 cm. long, 0.5–2 cm. wide; flowers sessile or with pedicels not over 4 mm. long, in several-flowered whorls; bracts ovate to linear, serrulate to entire, glabrate to long ciliate-pubescent, 3–10 mm. long, 1–5 mm. wide; calyx ciliate-pubescent to villous-pubescent throughout, 4–10 mm. long; calyx lobes lance-oblong, obtuse to acute, 1.5–6 mm. long, 1–3 mm. wide; corolla rose-purple to lilac or almost white, the veining darker colored and conspicuous, slightly declined, 7–20 mm. long; corolla tube 2.5–5 mm. long, 2–4 mm. wide; dorsal gibbous region shallow, 1–1.5 mm. deep, long-bearded within; upper lip paler than lower, purple-dotted below the sinus, 3.5–12 mm. long, the lobes rectangular, serrate-emarginate to entire, the sinus 1–5 mm. deep; reflexed region of upper lip 1.5–9 mm. long; lower lip 5–14 mm. long; keel 2 mm. shorter than lateral lobes, pale with brown-purple dots within at tip, 2–4 mm. deep; lateral lobes round-spatulate, emarginate to entire, 6–9 mm. wide, divergent; upper pair of filaments bearded to above the middle with bearding especially dense at place of attachment and on the very short appendage which is ca. 0.5 mm. long if present; lower filaments glabrous or bearded for one-third their length; stigma oblong but not definitely lobed; capsule 3.5–5 mm. long, scarcely exceeded by the calyx lobes; seeds many, flattened, rounded, slightly rugose-reticulate, 0.7–2 mm. long.

### Key to varieties

A. Lateral lobes of corolla emarginate, conspicuously wider than keel; sinus at least 2 mm. deep; flowers 9–20 mm. long; plant stout in appearance.

B. Corolla 15–20 mm. long; plant 15–35 cm. tall; seeds not over 1 mm. long. Central California

*3a. C. bartsiaefolia* var. *typica*

B. Corolla 9–13 mm. long; plant 7–20 cm. tall; seeds ca. 1.5 mm. long. North and west edges of Mojave Desert

*3b. C. bartsiaefolia* var. *davidsonii*

A. Lateral lobes of corolla entire, scarcely wider than keel; sinus less than 2 mm. deep; plant slender; seeds 1.5 mm. long

*3c. C. bartsiaefolia* var. *stricta*

*3a.* COLLINSIA BARTSIAEFOLIA var. **typica,** nom. nov.—*C. bartsiaefolia* Benth., in DC. Prodr. **10**:318. 1846; in Pl. Hartw., 328, no. 1885. 1839–1857; Gray Syn. Fl. No. Am. **2**:255. 1878; Jepson Man. Calif., 903. 1925 (in part); *C. bartsiaefolia* var. *alba* Orcutt, West. Amer. Sci. **7**:126. 1891; *C. hirsuta* Kellogg, Proc. Cal. Acad. **2**:110, *t.* 34. 1863.

Plant 15–35 cm. tall; corolla 15–20 mm. long; seeds small, not over 1 mm. long, restricted to central California.

**Type locality.**—Given by BENTHAM as "in montibus scopulosis," but the material collected by *Fremont* was all from California, probably the San Joaquin Valley.

**Representative material.**—CALIFORNIA: without locality, but without doubt from San Joaquin Valley, *Fremont* in 1844, type collection (G), in 1846 (G); Lakeport, *Bentley* in 1917, in part (S); Antioch, Contra Costa Co., *Ratton* in 1880 (S); Tracy, San Joaquin Co., *Baker* 2783 (P); Riverbank, Stanislaus Co., *Abrams* 9963 (S); 5 miles above Pollasky, Madera Co., *Heller* 8157 (S); Raymond, Madera Co., *Cummings* in 1896 (G); near Fresno, *Dudley* in 1900 (S); north of Bakersfield, *Cooper* in 1927 (P); Tulare Co., Kaweah, *Eastwood* in 1895 (G), Ducor, *Munz* 9041 (P); Del Monte, Monterey Co., *Heller* 6666 (P, S).

This plant is quite distinct from *bicolor* in its lack of long stamen appendages and in the conspicuous veining of the corolla lobes. Specimens from Keene, *Jones* in 1903 (P), and Fort Tejon, *de Vesey* 59 (G), may be cited as var. *typica* approaching var. *davidsonii*. They have the appearance of *davidsonii* but the seeds of *typica*.

*3b.* COLLINSIA BARTSIAEFOLIA var. **davidsonii** (Parish), comb. nov.—*C. davidsonii* Parish, Zoe **4**:147. 1893; Jepson Man. Calif., 903. 1925.

Plant smaller, not over 20 cm. high; stems often glabrate; flower 9–11 mm. long; seeds ca. 1.5 mm. long, often becoming slightly cup-shaped.

**Type locality.**—Lancaster, Mojave Desert.

**Material studied.**—CALIFORNIA: "Southern California," *Parry & Lemmon* 294 (G); Mojave Desert, *Pringle* in 1882 (G); Tejon Pass road, Mt. Piños region, *Dudley & Lamb* 4447 (S); Elizabeth Lake Canyon, Liebre Mts., *Dudley & Lamb* 4414 (S), west of Elizabeth Lake, *Peirson* in 1922 (P); ten miles south of Willow Springs, *Munz* 9994 (P); Antelope Valley, *Davidson* in 1895 (S), Lancaster, *Davidson* in 1893, type collection (G), *Dudley & Lamb* 4319 (S); Mojave River, near Hesperia, *Parish* 4984 (S), Los Flores Rancho, *Saunders* in 1906 (S).

This plant, which has heretofore been considered as a distinct species, seems to me to be only a small desert variety. Aside from the smaller habit, the main character that makes it of good varietal rank is the increased size of the seeds; otherwise, the morphology of the two varieties is identical.

3*c*. COLLINSIA BARTSIAEFOLIA var. **stricta** (Greene), comb. nov. —*C. stricta* Greene, Pittonia **2**:23. 1889; *C. tinctoria* var. *stricta* (Greene) Jepson Man. Calif., 903. 1925; *C. bicolor* var. ?, Benth. in Plantae Hartw., 328., no. 1884. 1839–57.

Resembling *typica* but more slender; flowers smaller, 8–9 mm. long; lateral lobes of corolla not emarginate and not much wider than keel; upper lip narrow, ca. 4 mm. long, sinus less than 2 mm. deep; seeds numerous, ca. 1.5 mm. long, often slightly cup-shaped.

**Type locality.**—"Bushy hills near Sheep Ranch, Calaveras Co."

**Material studied.**—CALIFORNIA: Calaveras Co., *Greene* in 1889, type collection (S); "in montibus Sacramento," *Hartweg* 1884 (G); Plumas Co., *Ames* in 1875 (?) (G); San Antonio Mission, Monterey Co., *Dudley* in 1895 (S); New Idria, San Benito Co., *Dudley* in 1899 (S).

Although this has been considered as a separate species by GREENE and as a variety of *tinctoria* by JEPSON because of the gibbous shape of the tube and the veining of the petals, it belongs very distinctly with *bartsiaefolia* in my opinion, even though the narrow lip is peculiar and variable. The general appearance of the plant, the distinct veining of the petals, and the shape, size, and number of the seeds suggest *bartsiaefolia*.

4. COLLINSIA CONCOLOR Greene, Erythea **3**:49. 1895; *C. bicolor* var. *concolor* (Greene) Jepson Man. Calif., 902. 1925.

Stems erect, occasionally diffusely branched, puberulent to glabrate, rarely glandular, 15–45 cm. tall; leaves thin, lanceolate-oblong, narrowly obtuse to acute, puberulent to glabrate, serrulate

and revolute to entire, scabrous-margined, cordate at base, 10–50 mm. long, 2–12 mm. wide; lower leaves smaller with petioles 2–20 mm. long; flowers sessile or with pedicels not over 4 mm. long, in several-flowered whorls; bracts linear, entire, puberulent to long ciliate-pubescent, 5–10 mm. long, 1–2 mm. wide; calyx scabrous-margined, pubescent above to villous-pubescent and submembranous below, 6–8 mm. long; calyx lobes oblong, broadly acute, 3–4 mm. long, ca. 1 mm. wide; corolla declined, appearing squarish-truncate, bluish lavender, 12–15 mm. long; corolla tube 3–5 mm. long, 3–4 mm. wide; dorsal gibbous region shallow, ca. 1.5 mm. deep, long-bearded within, especially toward the base; upper lip pale lavender to blue, 6–10 mm. long, reflexed from the 2-crested callous region; sinus 3–4 mm. deep, lobes truncate, emarginate, 3–4 mm. wide; triangular region between sinus and callosity spotted red-purple; lower lip deep lavender-blue, 8–11 mm. long; keel paler and yellowish at tip, sparsely bearded without, 2.5–4 mm. deep, ca. 1.5 mm. shorter than the lateral lobes; lateral lobes broadly spatulate, emarginate, divergent, sparsely bearded within, 3–6 mm. wide; upper pair of filaments bearded half way up, often with a rudimentary bearded basal appendage 0.5 mm. long; lower filaments rarely sparsely bearded near base; stigma not lobed; capsule 4 mm. long, usually well exceeded by calyx lobes; seeds flattened, irregularly round, rugose, ca. 1.5 mm. long, many in number (8–16).

**Type locality.**—"Witch Creek, San Diego Co."

**Some of specimens studied.**—CALIFORNIA: Yucaipa, San Bernardino Co., *Craig, Newsom, & Hilend* 367 (P); Idyllwild, Riverside Co., *Spencer* 2166 (P); Hemet Valley, *Munz & Johnston* 5532 (P); 20 miles N. of Idyllwild, *Jones* in 1926 (P); Dripping Spring, *Munz* 5100 (P); Palomar Mts., Oak Grove Trail, *Munz* 10395 (P); at Pine Hills, *Spencer* 373 (G,P); Warner's Hot Springs, *Munz* 9861 (P); Laguna Mts., *Munz* 8348 (P); Campbell Ranch, Laguna Mts., *Mearns* 3644 (S); Julian, *Brandegee* in 1894 (G,S); Witch Creek, *Alderson* in 1894, probably type material (G,S); Potrero Grade, *Munz & McCully* 8056 (P); Summit, W. of Jacumba, *Munz* 8043 (P); Campo, *Abrams* 3608 (S). LOWER CALIFORNIA: 45 miles S. E. of Tecate, *Munz* 9530 (P).

*C. concolor* has often been confused with *bicolor*, but it is easily distinguished from the latter by the lack of the long stamen appendage. If this is present at all, it is merely rudimentary. Then too, the flower of *concolor* has a square or truncate appearance, while in

*bicolor* the lobes are more rounded and spreading. The color of *bicolor* tends toward a lavender, that of *concolor* toward blue. In *bicolor* the region of reddish dots below the sinus of the upper lip varies from rounded to almost square, while in *concolor* it is triangular.

5. COLLINSIA BICOLOR Benth., Trans. Hort. Soc. N.S. 1:480. 1834.

Stems simple or diffusely branching, erect or somewhat reclining, glabrous to pubescent, occasionally sparsely glandular above, green to purplish, 10–50 cm. high; leaves green to reddish-purple, paler below, glabrous to pubescent, lanceolate-oblong, broadly acute, the base broad, margins serrulate to crenulate or entire, scabrous, 1–7 cm. long, 0.5–3 cm. wide; lower leaves more ovate, with petioles 2–10 mm. long; flowers sessile or with pubescent or often glandular pedicels 2–5 mm. long, in 2–7-flowered whorls; bracts lanceolate to linear, obscurely serrulate to entire, scabrous, glabrous to pilose-pubescent, 5–20 mm. long, 1–7 mm. wide, often becoming very leaf-like in lower whorls of inflorescence; calyx green to reddish-purple, submembranous, glabrous to long villous-pubescent, 5–10 mm. long; calyx lobes each 3-ribbed, linear to broadly lanceolate, narrowly obtuse to acute, glabrate (but scabrous-margined) to long villous-pubescent especially near base, occasionally sparsely glandular, 4–8 mm. long, 1–3 mm. wide; corolla declined, sparsely gland-bearded without, 1–2 cm. long; corolla tube 5–7 mm. long, 4–8 mm. wide; dorsal saccate region rounded, shallow, dark purple-lined, long bearded within, ca. 2 mm. deep; upper lip lilac to white, reflexed from the 2-crested transverse callosity, 3.5–12 mm. long, almost equaling to less than half as long as lower lip; upper lobes round-truncate, entire or retuse, often sparsely bearded within, 1.5–5 mm. wide, sinus 0.5–4 mm. deep, rounded region between the sinus and callosity spotted red-purple; lower lip violet or rose-purple to whitish, tips of lobes darker colored, sparsely bearded within, 6–14 mm. long; keel 1–2 mm. shorter than lateral lobes, 2–5 mm. deep; lateral lobes divergent, broadly spatulate, entire or emarginate, sparsely bearded within, 4–7 mm. wide; upper pair of filaments bearded half their length, possessing a linear bearded basal appendage ca. 2 mm. long and projecting into the base of saccate region of tube; lower filaments beardless; anther sacs dark purple; stigma not lobed;

capsule 4–7 mm. long, somewhat exceeded by calyx lobes; seeds flattened, ovate, rugose-reticulate, slightly winged, many in number, ca. 1.5–2 mm. long.

**Key to varieties**

A. Upper lip of corolla conspicuous, as long as or only slightly shorter than the lower lip; sinus of upper lip over 2 mm. deep
5*a*. *C. bicolor* var. *typica*

A. Upper lip of corolla short and recurved; sinus not over 2 mm. deep. Mountains of southern California
5*b*. *C. bicolor* var. *austromontana*

5*a*. C. BICOLOR var. **typica,** nom. nov.—*C. bicolor* Benth., Trans. Hort. Soc. N.S. **1**:480. 1834; in DC. Prodr. **10**:318. 1846; Curtis' Bot. Mag., *t.* 3488. 1838; Benth. Pl. Hartw., 328. no. 1883. 1839–57; Paxton's Mag. **3**:195; Gray Syn. Fl. No. Am. **2**:255. 1878; Jepson Man. Calif., 902. 1925; *C. heterophylla* R. Grah. in Hook. Bot. Mag. **65**:*t.* 3695. 1838; *C. multicolor* Lindl. & Paxt., Flow. Gard. **2**:89, *t.* 55. 1851–52.

Upper lip of corolla conspicuous, as long as or only slightly shorter than the lower lip; sinus of upper lip over 2 mm. deep.

**Type locality.**—CALIFORNIA.

**Representative material.**—CALIFORNIA: without locality, *Douglas*, probably type material (G), *Fremont* 442 (G), *Coulter* 602 (G); 20 miles north of Laytonville, Mendocino Co., *Munz* 9885 (P); Sulphur Banks, Lake Co., *Bowman* in 1902 (S); Lake Merced, San Mateo Co., *Elmer* 5046 (P,S); Santa Cruz, *Thompson* in 1902 (P,S); Stanford University, *Abrams* 2364 (P,S); foothills west of Los Gatos, *Heller* 7403 (S); New Idria, San Benito Co., *Abrams & Borthwick* 7968 (S); Monterey, *Eastwood* in 1900 (G); Point Piños near Pacific Grove, *Heller* 6578 (S); Paso Robles, *Munz* 10140 (P); Marysville Buttes, Butte Co., *Heller* 5559 (S); Caminetti Ranch near Jackson, Amador Co., *Mulliken* 101 (P,S); near French Flat, Tuolumne Co., *Ferris* 1510 (S); 3 miles from Oakdale, Stanislaus Co., *Abrams* 9967 (S); near Milo, Tulare Co., *Dudley* in 1900 (S); Los Angeles Co., South Hills near Pomona, *Munz* 2087 (P); Pasadena, *Jones* 3432 (P); Evey Canyon north of Claremont, *Johnston* in 1917 (P), San Gabriel Canyon, *Munz* 9410 (P); Lemon Tank, San Clemente Is., *Munz* 6686 (P); Sierra Canyon, Santa Ana Mts., *Munz & Harwood* 3747 (P); San Bernardino, *Parish* 263 (S); canyon near Murietta, Riverside Co., *Robinson & Crocker* in 1916 (P); above Escondido, *Munz & McCully* 8094 (P); San Diego, *Brandegee* 1709 (P); Witch Creek, *Abrams* 3782 (S). LOWER CALIFORNIA: without locality, *Jones* in 1882 (P); 10 miles north of Ensenada, *Canby* in 1925 (P); Coronado Is., *Cowles* in 1921 (P). MEXICO: Oaxaca, *Conzatti* in 1898 (G).

The *bicolor* group is very easily distinguished from all others by the long basal appendage to the upper filaments (*cf.* ALICE E. KEENER, BOT. GAZ. **20**:232. 1895). As to size of corolla and leaves, and the amount of pubescence, *typica* is extremely variable. The length of bracts also varies. Material from Oaxaca, Mex., might be of good varietal rank, because of the large whorled bracts which make the corollas inconspicuous, but it is here included in *typica* because of lack of sufficient material for thorough study. The color of the corolla varies from almost entirely white to conspicuously lavender or deep purple, with the upper lip of the corolla usually paler.

The following specimens may be cited as intermediates between *typica* and *austromontana*.—Cobb Mt., Lake Co., *Leithold* in 1893 (S); Mt. Diablo, *Abrams* 8029 and 8055 (S); Petrified Forest, Sonoma Co., *Heller* in 1902 (S); near San Bernardino, *Parish* in 1901 (S), *Parish* 11216 (P); Los Angeles Co., hills above Claremont, *Jones* in 1926 (P); Little Santa Anita Canyon, *Abrams* 2613 (S); Mt. Lowe, *Diehl* 243 (P); hills near Pasadena, *Jones* in 1902 (P); San Diego Co., San Diego, *Dunn* in 1891 (S), *Fernald* in 1896 (G); Pine Hills, *Spencer* 1616 (P).

5*b*. C. BICOLOR var. **austromontana,** var. nov.

Labium superiore breve, reflexum; sinu non plusquam 2 mm. lato.

**Type,** near Brown's Flats, San Gabriel Mts., Los Angeles County, California, *Johnston* 1750 (Pomona College Herbarium no. 4314; cotypes at Pomona and Stanford).

**Specimens studied.**—CALIFORNIA: San Gabriel Mts., Lower San Sevaine Flats, *Johnston* 1750 (P), 4122 (P); on old road to San Sevaine Flats, *Johnston* in 1925 (P); Cucamonga Canyon, *Johnston* in 1919 (P), *Davis* in 1915 (P); Stoddard's Canyon, *Jones* in 1924 (P); Big Santa Anita Canyon, *F. Grinnell Jr.* in 1917 (S); San Bernardino Mts., south slope, *Parish* in 1895 (S); North Fork of Deep Creek, *Abrams & McGregor* 718 (S); Santa Ana Canyon, *Jaeger* in 1925 (P); Julian, San Diego Co., *McGregor* in 1918 (S).

Confused with *tinctoria* because of the short upper lip, var. *austromontana*, because of the long filament appendages, must be included in *bicolor*. Only the material with the extremely short upper lip is classed as *austromontana*, and the numerous intergradations between this and *typica* with the long upper lip are classed as intermediates, and have been cited under *typica*. True *austromontana* is restricted to the mountains of southern California, but some of the intermediates extend into the central part of the state.

6. COLLINSIA GREENEI Gray, Proc. Am. Acad. **10**:75. 1874; Syn. Fl. No. Am. **2**:256. 1878; Jepson Man. Calif., 903. 1925.

Stems slender, diffusely branching, puberulent to villous-pubescent and glandular, 10–30 cm. long; leaves oblong-linear, tapering to apex, broadly acute, dentate or denticulate, glabrous to puberulent, 7–30 mm. long, 2–7 mm. wide; lower leaves more ovate with petioles ca. 1 cm. long; pedicels 1–5 at a node, glandular-puberulent, 2–10 mm. long; bracts linear, sparsely dentate to entire, puberulent to glandular, 3–10 mm. long, ca. 1–2 mm. wide; calyx puberulent to glandular-pubescent, 4–7 mm. long; calyx lobes lanceolate, narrowly obtuse to acute, 2–4 mm. long, ca. 1 mm. wide; corolla "deep azure-blue," 10–12 mm. long; corolla tube ca. 6 mm. long, 4–5 mm. wide; dorsal gibbous region shallow, 1 mm. deep, short-bearded; throat open; upper lip shorter than lower, 4–5 mm. long, reflexed region ca. 2 mm. long, the lobes rounded, sinus 1 mm. deep and subtended by a two-crested transverse callous ridge, and extended down each side of lip forming conspicuous lateral crests, these crests ca. 1 mm. long and almost as wide; lower lip 5–6 mm. long; small lateral lobes scarcely as long as the keel, spatulate, ca. 5 mm. long, 1.5 mm. wide; keel 3 mm. deep; lateral saccate region sparsely gland-bearded within; upper pair of filaments glabrous or sparsely bearded at base; stigma not lobed; capsule 4 mm. long, just exceeded by calyx lobes; seeds few, normally 4, oblong, flattened or cup-shaped, smooth, 2–3 mm. long.

**Type locality.**—Crevices of rocks, mountains of Lake Co.

**Material studied.**—CALIFORNIA: Trinity Co., without locality, *Rattan* in 1883 (G), between the forks of Trinity River, *Rattan* in 1883 (S); west slope of Black Butte, Mendocino Co., *Rattan* in 1884 (G,S); Glenn Co., 9 miles east of Alder Springs, *Heller* in 1914 (S); between Mud Flat and Bennett Springs, *Heller* 11551 (S); Lake Co., mountains, crevices of high rocks, *Greene* in 1874, type collection (G); near Blue Lakes *Tracy* 1677 (S), Mt. Sanhedrin, *Eastwood* 12889 (P); Mt. Hull, *Hall* 9531 (P); Geysers, Sonoma Co., *Bolander* 3968 (G).

The four conspicuous lateral and transverse callous crests of the upper lip which extend into the throat characterize this species. Pedicel length is so variable that *greenei* may be placed in either the sessile group or the group with pediceled flowers.

7. COLLINSIA FRANCISCANA Bioletti, Erythea **1**:17. 1893; Jepson

Man. Calif., 903. 1925; *C. sparsiflora* var. *franciscana* Jepson Fl. W. Middle Calif., 399. 1901.

Plant diffusely branched, "erect or reclining on neighboring plants," glabrous below to glandular-pubescent and often viscid above, 20–60 cm. tall; leaves deltoid-ovate to lance-ovate, acute, serrate to serrulate, scabrous-margined, glabrous to sparsely pubescent, 1–5 cm. long, 0.5–3 cm. wide, becoming gradually reduced in the inflorescence to small linear bracts in uppermost whorls; lower leaf petioles 1–2 cm. long; pedicels glandular-pubescent, 0.2–4 cm. long; upper flowers in several-flowered whorls; lower flowers long-pediceled and 1–3 at a node; calyx viscid-pubescent, submembranous, 5–11 mm. long; calyx lobes broadly lanceolate, acute, 2–5 mm. long, 1–3 mm. wide; corolla 12–18 mm. long; corolla tube 5–6 mm. long, 4–5 mm. wide; dorsal saccate region shallow, ca. 1 mm. deep, bearded; upper lip white, purple-spotted at base, 6–10 mm. long; upper lobes ovate-truncate, emarginate, 4–6 mm. wide; sinus 2–3.5 mm. deep; lower lip bluish-purple, sparsely bearded without, 9–13 mm. long; keel 3–4 mm. deep, 1–2 mm. shorter than lateral lobes; lateral lobes obovate, emarginate, 4–7.5 mm. wide; upper pair of filaments bearded, clubbed at base or with appendage ca. 0.5 mm. long; gland often on a very short, bearded base; stigma not lobed; capsule 4–7 mm. long; seeds 8 or more, irregularly round-oblong, flattened when immature but becoming thickened, rugose, 1.5 mm. long.

**Type locality.**—San Francisco peninsula.

**Specimens studied.**—CALIFORNIA: San Francisco Co., *Michener & Bioletti* in 1893, probably type material (P,S); Sutro Woods, *Walker* 1067 (P); Mission Hills, *Bolander* 148 (G); San Mateo Co., San Bruno Hills, *Heller* 8463 (S); between San Mateo and Half Moon Bay, *Heller* 8580 (S); Crystal Springs Lake, *Baker* 647 (P); Santa Clara Co., Stanford University, *Elmer* 5050 (S,P); Serpentine Hills near Edenvale, *Ferris* 806 (S); Pacific Grove, Monterey Co., *Elmer* 4686 (P,S).

*C. franciscana* has been confused with *bicolor* and *bartsiaefolia*, but can be distinguished from both by the elongate pedicels. The general appearance is that of *bicolor*, but the stamen appendages are merely rudimentary. The leaves are thin, and triangular as compared with the thickened lance-oblong leaves of *bartsiaefolia*.

8. COLLINSIA VERNA Nutt., Jour. Acad. Philad. 1:190, *t.* 9.

1817; Benth. in DC. Prodr. 10:318. 1846; Gray Syn. Fl. N. Am. 2:256. 1878; *C. bicolor* Raf., Cincinnati Lit. Gaz. (for Neophyton 2), 84. 1824; *C. bicolor* var. *latifolia* Raf., *l.c.*; *C. bicolor* var. *cordata* Raf., *l.c.*; *C. bicolor* var. *rotundifolia* Raf., *l.c.*; *C. bicolor* var. *verticillata* Raf., *l.c.*; *C. bicolor* var. *integrifolia* Raf., *l.c.*; *C. bicolor* var. *angustifolia* Raf., *l.c.*; *C. alba* Raf., *l.c.*

Stems erect, branching or simple, glabrous below to puberulent above; leaves ovate to deltoid-lanceolate, obtuse to acute, often cordate and clasping at base, crenulate to entire, scabrous, 1–6 cm. long, 0.5–2 cm. wide, becoming gradually reduced to small linear bracts in uppermost whorls of inflorescence; basal leaves usually shorter and broader than cauline leaves, with petioles 1–3 cm. long; flowers 4–6 at a node above, 1–3 below; pedicels nearly erect, puberulent, 0.5–3 cm. long; calyx somewhat pale and submembranous at base, puberulent-glabrate, ciliate-pubescent, 5–8 mm. long; calyx lobes lanceolate, acute, 4–5 mm. long, 1–2 mm. wide; corolla declined, 8–14 mm. long, upper lip white or lavender-tinged, lower lip bright blue; corolla tube ca. 4 mm. long, 2–3 mm. wide; dorsal gibbous region shallow, 1 mm. deep, sparsely short-bearded near base; upper lip almost as long as or 2–3 mm. shorter than lower lip, 6–8 mm. long, 2–3 mm. wide, with region below sinus yellowish and spotted with saffron, sinus 4–5 mm. deep; upper lobes obovate, emarginate, 2–4 mm. wide; lower lip 7–10 mm. long; keel about 3 mm. deep, sparsely bearded without, 1.5–3 mm. shorter than lateral lobes; lateral lobes obovate, emarginate, 3–6 mm. wide; upper filaments bearded for half their length and at base, lower filaments beardless or occasionally sparsely bearded near base; anther sacs yellow; stigma not lobed; capsule 4–5 mm. long, exceeded by calyx lobes; seeds 4 or less, round-oblong, somewhat flattened when immature, becoming thickened, rugose-reticulate, 1.5–2.5 mm. long.

**Type locality.**—near Gallipolis, Ohio.

**Material studied.**—NEW YORK: Buffalo, in 1887, collector not known (G). PENNSYLVANIA: Allegheny Co., *Knife* in 1871 (G). KENTUCKY: Lexington, *Short* in 1856 (G). OHIO: Erie Co., *Moseley* in 1903 (G); Licking Co., *H. L. Jones* in 1891 (G); Portage Co., *Webb* in 1923 (G); Black River, Cook (P). MICHIGAN: Olivet, *Denslow* in 1875 (G); Agricultural College, *Baker* in 1890 (P); Hubbardston, *Smith* in 1876 (S), *Wheeler* in 1873 (P). INDIANA: Crawfordsville, *Evans* (S); Hanover, *Young* in 1875 (P); Bluffton, Wells Co., *Deam* in

1907 (G,P). ILLINOIS: Somer, Champaign Co., *Pease* in 1909 (G); Chicago, *Hitchings* in 1890 (G); Decatur, *Gleason* in 1897 (G); Bloomington, *Robinson* in 1884 (G); Makanda, *Baker* in 1900 (P). IOWA: Jefferson Co., *Fitzpatrick* in 1896 (G). MISSOURI: Jefferson Co., *Eggert* in 1887 (G); Cass Co., *Broadhead* (S); Vale, *Bush* 4931 (G). LOUISIANA: without locality, *ex* Herb. *George Thurber* (G).

The main distinguishing characters for this species as compared with *C. violacea* are the size and number of seeds. The upper lip ordinarily almost equals the lower in length, but this is variable, and the upper lip becomes quite noticeably shorter in some specimens, thus approaching that in *violacea*. Then, too, the upper lip is not consistently white, often becoming tinged with lavender as in *violacea*. The leaves are quite variable in size and length, but are rather broader than in *C. violacea*. The corolla lobes are not as deeply notched, although there are some specimens that would rather easily fit in as intermediates between the two species in this respect. Taking typical material of the two, however, they are different in the above respects, and may well be termed separate species, although they are closely allied.

RAFINESQUE took up for *verna* the name *C. bicolor* (Cincinnati Lit. Gaz. 84. 1824), claiming that the plant had been given this specific name as early as 1810 by MILLER and MUHLENBERG under the genus *Herpestis*. Since no evidence has been found of the publication of the name *bicolor* previous to that of *verna*, the name *bicolor* of RAFINESQUE is here considered a synonym.

9. COLLINSIA VIOLACEA Nutt., Trans. Am. Phil. Soc. **5**:179. 1837; Benth. in DC. Prodr. **10**:318. 1846; Gray Syn. Fl. No. Am. **2**:256. 1878.

Plants erect, branched or simple, puberulent, 10–35 cm. tall; leaves thickened, oblong to lance-oblong, obtuse to acute, serrulate to entire, scabrous, pubescent, 1–4 cm. long, 0.2–1.5 cm. wide; cauline leaves gradually reduced to small linear bracts in upper inflorescence; basal leaves often ovate, with petioles as long as leaves; flowers 4–6 at a node above, 1–3 below; pedicels nearly erect, puberulent, 0.5–2 cm. long, shorter ones in upper whorls; calyx purplish below, not conspicuously submembranous, pubescent, 5–8 mm. long; calyx lobes lanceolate, acute to obtuse, 3–5 mm. long, 1–1.5 mm. wide; corolla declined, bright violet, upper lip paler,

10–15 mm. long; corolla tube 4–5 mm. long, 2–3 mm. wide, bearded below the lower filaments and around gland; dorsal gibbous region shallow, ca. 1 mm. deep; upper lip 4–6 mm. long, ca. 2 mm. shorter than lower lip, with crested region "marked with reniform yellowish fulvous spot"; sinus 2–3 mm. deep; upper lobes ca. 3 mm. wide, obcordate, notch approaching 1 mm. in depth; lower lip 6–9 mm. long; keel ca. 1 mm. shorter than lateral lobes; lateral lobes 5–6 mm. wide, obovate, obcordate, notch 1 mm. deep; upper filaments bearded for half their length; stigma rather large, not definitely lobed; capsule 4–5 mm. long, exceeded by calyx lobes; seeds flattened when immature, becoming round-oblong and thickened, rugose-reticulate, ca. 1–1.5 mm. long, 6–12 in number.

**Type locality.**—On the hills and upland woods of the Arkansas and Red rivers.

**Specimens studied.**—MISSOURI: Carthage, *Palmer* in 1903 (G); Swope Park, *Bush* in 1923 (P). KANSAS: Cherokee Co., *Hitchcock* 979 (G). ARKANSAS: without locality, *Harvey* in 1880 (G), *Pitcher* in 1877 (G); Fayetteville, *Harvey* in 1879 (G). OKLAHOMA: near Crusher Spur, Murray Co., *Stevens* in 1913 (G,S); Eufaula, *Brainerd* in 1908 (G). TEXAS: Elmo, *Reverchon* 3935 (G).

The seeds of this species are smaller and more numerous than in *verna*. Its range somewhat overlaps that of *verna*, but the two species are definite in seed characters, and can usually be distinguished also by several gross corolla characters.

10. COLLINSIA SPARSIFLORA Fisch. & Mey., Ind. Sem. Hort. Petrop. **2**:33. 1836.

Stems slender, branched near base or simple, often reddish, glabrous or slightly puberulent, 7–40 cm. tall; leaves glabrous to sparsely puberulent, serrulate to entire, scabrous-margined, linear to oblong, narrowly obtuse, 8–20 mm. long, 1–5 mm. wide, gradually transitional to small linear bracts in upper inflorescence; basal leaves broader and shorter with petioles 5–10 mm. long; flowers 1–2 (rarely 3) at a node, on slender pedicels 5–25 mm. long; calyx submembranous and reddish at base, glabrate, setulose-margined, 5–9 mm. long, from one-third as long as to fully as long as the corolla; calyx lobes ovate or deltoid-lanceolate to linear, acute, 2–5 mm. long, 0.5–2 mm. wide; corolla strongly declined, dorsal side of tube forming almost a right angle with pedicel, or erect and in a straight line with

the pedicel, pale lavender to purple, 5–15 mm. long; corolla tube 3–9 mm. long, 2–7 mm. wide; dorsal region of tube strongly gibbous (and 1–2 mm. deep) to straight, usually sparsely bearded within; upper lip purple-dotted above the callous crests, 2–9 mm. long, sinus 1–3 mm. deep; upper lobes truncate, retuse or emarginate in large-flowered forms, oblong and entire in small-flowered forms, 1–5 mm. wide; lower lip 3–11 mm. long; keel 1–4 mm. deep, usually at least 1 mm. shorter than the lateral lobes, more or less long-bearded without near tip; lateral lobes spatulate, emarginate to entire, 1–5 mm. wide; upper pair of filaments at least sparsely bearded for half their length and often bearded at base; lower filaments glabrous or occasionally bearded near base; stigma somewhat 2-lobed; capsule 3–5 mm. long, more or less exceeded by calyx lobes in fruit; seeds 4–8, round-oblong, somewhat flattened, often acutely wing-margined, rugulose, 2–2.5 mm. long when mature.

**Key to varieties**

A. Seeds 5–8; mature capsule 4–5 mm. long.

B. Corolla strongly declined; dorsal side of saccate tube forming right angle with pedicel; calyx ca. $\frac{1}{3}$ ($\frac{1}{2}$) the corolla length, lobes subulate, not concealing and scarcely exceeding the saccate tube.

C. Corolla over 12 mm. long . . 10*a*. *C. sparsiflora* var. *arvensis*

C. Corolla 9–12 mm. long . . . . . 10*b*. *C. sparsiflora* var. *typica*

B. Corolla not strongly declined; dorsal side of tube gibbous or in straight line with pedicel; calyx from half as long as to fully as long as corolla, lobes lanceolate to linear, well exceeding and concealing the gibbous region of tube.

C. Corolla 9–13 mm. long; calyx 7–12 mm. long, cleft at least $\frac{2}{3}$ of its length; stems simple or branched, erect-appearing. Vicinity of Columbia River south to Butte and Lake counties, California . . . . . 10*c*. *C. sparsiflora* var. *brucae*

C. Corolla 6–9 (–10) mm. long; calyx 4–7 mm. long, cleft $\frac{1}{2}$ to $\frac{2}{3}$ its length; stems divaricately branched. Central California . . . . . 10*d*. *C. sparsiflora* var. *solitaria*

A. Seeds 4; mature capsule 3–3.5 mm. long; corolla ca. 5 mm. long; bearding on filaments often sparse. Sierran and north-central

California.....10*e*. *C. sparsiflora* var. *collina*

10*a*. C. SPARSIFLORA var. ARVENSIS (Greene) Jepson, Fl. W. Middle Calif., 398. 1901; Man. Calif., 904. 1925; *C. arvensis* Greene, Pittonia **2**:232. 1892.

Plants occasionally 35 cm. tall; corolla 12–20 mm. long.

**Type locality.**—Knight's Valley, Sonoma Co., and adjacent Lake and Marin Cos.

**Specimens seen.**—CALIFORNIA: Mendocino Co., *Purdy* in 1882 (S); Ukiah, *Bolander* 4642 (G); Lake Co., Lower Lake, *Bowman* 109 (S); Clear Lake, *Peirson* 6584 (P); Napa Co., Calistoga, *Baker* 1984 (P); Napa Valley, *Thurber* 502 (G), *Greene* 87 (G); Sonoma Co., Knight's Valley, *Eastwood* in 1900 (G); Kenwood, *Michener & Bioletti*, in 1893 (P,S); hills southeast of Santa Rosa, *Heller & Brown* 5117 (G,P,S); Healdsburg, *Rattan* in 1880 (S); Fort Ross, *Heller* 6601 (P,S); Marin Co., Martinez, *Rattan* in 1880 (S).

This variety is easily distinguished by the conspicuously large size of the corolla as compared with others of the group.

10*b*. C. SPARSIFLORA var. **typica,** nom. nov.

*C. sparsiflora* Fisch. & Mey., Ind. Sem. Hort. Petrop. **2**:33. 1836; Gray Syn. Fl. No. Am. **2**:256. 1878; Jepson Man. Calif., 904. 1925; *C. parviflora* var. *sparsiflora* Benth. in DC. Prodr. **10**:319. 1846; Plantae Hartw., 328. 1839–57.

Calyx one-third (to one-half) the corolla length, lobes subulate, not concealing and scarcely exceeding the saccate base of corolla tube; corolla 9–12 mm. long, strongly declined, dorsal side of tube forming a right angle with pedicels.

**Type locality.**—Vicinity of Fort Ross.

**Material studied.**—Without locality, *Fremont* 234 (G), "Ross," Herb. Acad. Petrop., without doubt from Fort Ross, type material (G). CALIFORNIA: Ukiah to Largo, *Abrams* 7001 (S); Sonoma Co., Healdsburg, *Rattan* in 1880 (S); Bodega Bay, *Heller & Brown* 5268 (P,S); Petaluma, *Congdon* 76 (G), *Smith* 1380 (S); Santa Rosa, *Bolander* 3810 (G); Santa Rosa to Calistoga, *Chandler* 7549 (P); near Vallejo, Solano Co., *Greene* 63 (G); Martinez, Contra Costa Co., *Rattan* in 1880 (S).

Variation has its extreme representation in the *sparsiflora* group. The size of the corolla, shape of the tube, and characters of the corolla lobes are so variable that there is ample reason for several varieties, yet because of numerous intergradations none of these seems distinct enough for specific rank. In *sparsiflora* var. *typica* we find a comparatively small portion of the whole group repre-

sented. Study of the type brings to light the fact that much of the material formerly classed as *sparsiflora* is worthy of varietal rank. The strongly declined corolla with saccate tube, and the length of the flower separate this variety from the others.

The following specimens may be cited as representing intergradations between *typica* and *brucae*.—CALIFORNIA: Mt. St. Helena, *Eastwood* 11751 (P); Mt. Sanhedrin, *Eastwood* 12799 (P); Mt. Tamalpais, Marin Co., *Grant* 926 (S), *Abrams* 8070 (S); Contra Costa Co., Antioch, *Davy* 961 (S); Byron, *Bioletti* in 1892 (S); Solano Co., Vacaville, *Platt* in 1898 (P); Elmira, *Rattan* in 1878 (S).

10*c*. C. SPARSIFLORA var. **brucae** (Jones), comb. nov.—*C. brucae* Jones, Contr. West. Bot. **12**:69. 1908.

Stems simple or branched, appearing erect; calyx from half as long as to fully as long as corolla, cleft one-half to two-thirds its length, lobes lanceolate to linear, well exceeding and concealing the gibbous region of the corolla tube; corolla 9–13 mm. long, not strongly declined, often in a straight line with the pedicel, and appearing tubular; corolla lobes not conspicuous.

**Type locality.**—Not given, but without doubt Little Chico, Butte Co.

**Specimens studied.**—WASHINGTON: Klickitat Co., near Bingen, *Suksdorf* 2772 (S); White Salmon, *Suksdorf* 298 (G). OREGON: Rogue River Valley, *Howell* 653 (G); The Dalles, *Howell* in 1882 (S), *Sheldon* 10214 (P,S), *Peck* 3879 (G). CALIFORNIA: Siskiyou Co., near Yreka, *Greene* 730 (G); Shasta Valley, *Buller* 574 (P); Buck Mt., Humboldt Co., *Tracy* 4685 (P); Butte Co., Little Chico, *Bruce* 2063, without doubt type material (G,P,S); Chico, *Bidwell* in 1878 (G), *Heller* 11190 (S); near Clear Creek, *Brown* 161 (S); Sulphur Banks, Lake Co., *Bowman* 162 (S).

This variety seems to be a distinct segregate from *typica*, with a few intergrades from intermediate localities. The long calyx, quite concealing a goodly portion of the corolla, the slightly gibbous corolla tube, and the tubular appearance of the flower separate it from *typica*, while the size of the corolla is the main distinction between *brucae* and *solitaria*.

10*d*. C. SPARSIFLORA var. **solitaria** (Kellogg), comb. nov.—*C. solitaria* Kellogg, Proc. Cal. Acad. **2**:110. 1863; *C. divaricata* Kellogg, *l.c.* **3**:36. 1863.

Plant divaricately branching; calyx 4–7 mm. long, cleft half to two-thirds the corolla length; corolla 6–9 mm. long, tube gibbous or straight.

**Type locality.**—Vicinity of Oakland.

**Material studied.**—CALIFORNIA: Mokelumne Hill, Calaveras Co., *Blaisdell* (S); Table Mt. above Rawhide, Tuolumne Co., *Ferris* 1482 (S); Marin Co., *Brewer* 929 (G); Saucilito Hills, *Kellogg* 662, type of *divaricata* (G); San Francisco, *Eastwood* in 1895 (G); Mission Hills, *Rattan* in 1881 (S); San Mateo Co., Lake San Andreas, *Abrams* 2322 (P,S); Crystal Springs Lake, *Baker* 444 (P); Santa Clara Co., Mt. Hamilton, *Heller* 8539 (S), *Elmer* 4718 (S), *Baker* 641 (P); Stanford University, *Atkinson* in 1900 (S); near Frenchman's Lake, *Dudley* in 1893 (S); south of Gilroy Hot Springs, *Dudley* in 1910 (S); Monterey Co., between Goold Creek and Burnett Creek, *Dudley* in 1901 (S); near Jones Ranch, Santa Lucia Mts., *Ferris* 1834 (P,S), Santa Lucia Mts., *Plaskett* 94 (G); Fremont's Peak, San Juan, San Benito Co., *Elmer* 5048 (S); Atascadero Creek, San Luis Obispo Co., *Munz* 9221 (P); S.W. of Coalinga, Fresno Co., *Munz* 9176 (P).

Although the calyx length is somewhat variable in this variety, it is at least half the length of the corolla, except in specimens from Lake San Andreas (*Abrams*) in which it is one-third as long as the tubular corolla. Size and shape of corolla are variable, but both the corolla length and the divaricately branching habit make *solitaria* distinct.

10*e*. C. SPARSIFLORA var. **collina** (Jepson), comb. nov.—*C. parviflora* var. *collina* Jepson Man. Calif., 904. 1925.

Plant slender, erect or divaricately branched, leaves ca. 1 cm. long; calyx almost equaling corolla length, lobes lance-linear; corolla ca. 5 mm. long, tube gibbous or straight; bearding on upper filaments often sparse; mature capsule 3–3.5 mm. long; seeds 4.

**Type locality.**—Penn Valley, foothills of Nevada Co.

**Specimens studied.**—CALIFORNIA: fields of Butte Co., *Bruce* 2062 in part (P); Lakeport, *Bentley* in 1917 (S); Sacramento, *Brown* in 1903 (S), *Hannibal* in 1918 (S); Live Oak, San Joaquin Co., *Rattan* in 1883 (S); El Dorado Co., *Rattan* in 1866, in part (S); between Clarksville and Shingle Springs, *Heller* 12289 (S); Kelsey, *Jones* in 1903 (P); Stoney Creek, Amador Co., *Hansen* 1525 (S); Penn Valley, Nevada Co., *Jepson* in 1892, type collection (J).

This slender small-flowered variety is distinguishable by the number of seeds and the slightly smaller capsule. It is to be referred to this species rather than to *parviflora* because of its bearded stamens; its corolla characters, too, place it in this group.

11. COLLINSIA PARRYI Gray Syn. Fl. N. Am. **2**:257. 1878; Jepson Man. Calif., 904. 1925; *C. cahonis* Jones, Contr. West. Bot. **12**:68. 1908.

Plants erect or diffusely branched, retrorse-puberulent, 9–45 cm. tall; leaves lanceolate to lance-linear, obtuse to acute, sessile or with petiole 1–2 mm. long, glabrate, serrate to entire, 5–45 mm. long, 1–12 mm. wide, becoming gradually reduced to small linear bracts in uppermost whorls of inflorescence; lower leaves ovate to oblong, obtuse, with petioles 0.5–2 cm. long; flowers 2–3 (1–5) at a node; pedicels retrorse-puberulent, 0.5–4.5 cm. long, subtended by leaves; calyx retrorse-puberulent, ciliate-pubescent, 4–7 mm. long, at least equaling the length of corolla tube; calyx lobes broadly lanceolate, somewhat obtuse, 2–3 mm. long, ca. 1.5 mm. wide; corolla declined, lavender-blue, 5–10 mm. long; corolla tube paler, 3–5 mm. long, 2–4 mm. wide; dorsal gibbous region shallow, ca. 1 mm. deep, rather long-bearded within; upper lip 3–5 mm. long, its sinus 1–2 mm. deep, subtended by a triangular purple-dotted callous region from which the truncate-emarginate (rarely entire) lobes 1.5–2 mm. wide fold back; lower lip 4–7 mm. long; keel about 1 mm. shorter than the lateral lobes, 1–1.5 mm. deep; lateral lobes broadly spatulate, emarginate (rarely entire) 1.5–3 mm. wide; lateral sac occasionally gland-bearded; upper pair of filaments bearded for half their length (occasionally sparsely so); lower filaments glabrous or rarely sparsely bearded at base; stigma not lobed; capsule 4–5 mm. long, scarcely exceeded by calyx lobes; seeds 8–12, round-oblong, flattened when immature, thickened at least on edges when mature, rugulose, tan, ca. 1 mm. long.

**Type locality.**—San Bernardino Co., California.

**Specimens studied.**—CALIFORNIA: without locality, *Coulter* 597 (G), *Parry* 221 (G); Santa Monica, *Hasse* in 1890 (S); Soldier's Home, Los Angeles Co., *Hasse* in 1890 (G); Newhall, *Hasse* in 1892 (G), *Hasse* in 1893 (S); Pasadena, *Grant* in 1900 (P,S); Verdugo Hills, *Abrams* 1404 (S); San Gabriel Mts., San Gabriel Canyon, *Munz* 9432 (P), at foot of canyons north of Claremont, *Quibell* in 1927 (P); San Antonio Canyon, *Peirson* in 1920 (P); Lytle Creek Canyon, *Munz* 8153 (P); Cajon Pass, *Jones* in 1903, type of *cahonis* (not from Tehachapi, as given in type description) (P); San Bernardino Co., *Lemmon* 1178 (G), *Parry & Lemmon* in 1876, type collection (G); San Bernardino Mts., *Parish* 912 (G,S); Waterman Canyon, *Jones* in 1926 (P); below Seven Oaks, *Newsom* in 1926 (P).

This species is distinct enough, but probably a segregate of the *sparsiflora* group. The bearding on the filaments, the numerous

seeds that are thickened when mature, and the limited geographical range separate it from other species with which it might be confused. Specimens from two regions are peculiar. Those from Cajon Pass (*Jones*) and Newhall (*Hasse*) are rather succulent and approach the broadened calyx of *C. callosa*, while those from Soldier's Home (*Hasse*) and Santa Monica (*Hasse*) often have very sparse bearding on the stamens, and the upper and lower lateral lobes of the corolla are entire and not emarginate.

12. COLLINSIA PARVIFLORA Dougl. in Lindl., Bot. Reg. 13:t. 1082. 1827; Benth. in DC. Prodr. 10:318. 1846; Gray Syn. Fl. No. Am. 2:256. 1878; Jepson Man. Calif., 904. 1925; *C. minima* Nutt., Jour. Acad. Philad. 7:47. 1834; *C. pauciflora* of Hook. Fl. Bor. Am. 2:94. 1838; *C. tenella* of Piper, Contr. U.S. Nat. Herb. 11:496. 1906.

Stems ascending or erect, branched, glabrate to puberulent, often inconspicuously glandular, 5–40 cm. tall; leaves serrulate to entire, glabrate-puberulent or sparsely glandular, often purplish below, 0.7–5 cm. long, 2–8 mm. wide; oblong to lance-linear, becoming smaller and linear-bracteate in inflorescence and ca. 5 mm. long in uppermost whorls; lower leaves ovate to oblong-ovate with petioles 5–10 mm. long; flowers 2–5 in a whorl above, usually solitary below; pedicels puberulent to glandular-pubescent, 3–15 mm. long; calyx somewhat membranous below, puberulent to glabrate, scabrous-margined, 3–7 mm. long, from half as long as to almost equal the corolla length; calyx lobes subulate to linear-lanceolate, acuminate-acute, ca. 1 mm. wide; corolla declined to almost erect, 4–6 mm. long, tube white to pale blue, lobes a clear blue, often pale, upper lip varying to white; corolla tube half the length of the corolla, throat compressed, making the tube seem two-thirds the corolla length; dorsal gibbous region abrupt but shallow, ca. 0.5 mm. deep, short-bearded to glabrous; upper lip 2–3 mm. long, sinus ca. 1 mm. deep, lobes obovate-spatulate, slightly recurved from crested region; lower lip 2.5–3.5 mm. long; keel 1 mm. deep, ca. 1 mm. shorter than lateral lobes; lateral lobes spatulate, ca. 1 mm. wide; filaments rather stout, glabrous; stigma 2-lobed; capsule 3–4 mm. long, slightly exceeded by calyx tips; seeds normally 4, 1–2 mm. long, round-oblong, thick, smooth, reddish-brown or brown.

**Type locality.**—Vicinity of Columbia River.

**Representative material**[1].—CANADA: Vancouver Is., Victoria, *Macoun* 54 (G); Comox, *Macoun* 717 (G); Bald Mt., Cowichan Lake, *Rosendahl* 1833 (G); Selkirks, B.C., *Brown* 293 (G); Field, B.C., *Brown* 347 (G); Banff, Alta., *Moodie* 1237 (G); Lake Winnepeg Valley, *Bourgeau* in 1851 (G). WASHINGTON: Humptulips City, *Lamb* in 1897 (S); Button Springs, *Leiberg* 354 (G,P); Conconully, *Jones* in 1911 (P); Pullman, *Duthie* (S); Swauk River, Kittitas Co., *Sharples* 224 (G). OREGON: Multnomah Co., *Howell* 265 (G); Redmond, *Whited* in 1912 (S); 25 miles southeast of Pendleton, *Munz* 9914 (P); Grant's Pass, *Prescott* in 1912 (G). CALIFORNIA: Yreka, *Butler* 1133 (P,S); Little Hot Springs Valley, Modoc Co., *Baker & Nutting* in 1894 (S); Kneeland Prairie, Humboldt Co., *Rattan* in 1882 (S), *Tracy* 2658 (S); Prattville, *Heller & Kennedy* 8808 (S); Jonesville, Butte Co., *Heller* 12048 (S); Fallen Leaf Lake, El Dorado Co. (S); Emigrant Gap, *Jones* 3293 (P); Reverse Creek, Silver Lake Region, *Peirson* 6136 (P); lower end of Donner Lake, *Heller* 6867 (P,S); Bonita Meadow, Tulare Co., *Hall & Babcock* 5186 (S); San Bernardino Mts., Bear Valley, *Parish* 3754 (G), *Munz* 8189 (P), South Fork of Santa Ana River, *Peirson* 3141 (S); San Jacinto Mts., *Hall* 1810 (S); south of Cuyamaca Lake, *Munz & McCully* 8124 (P); Laguna Mts., San Diego Co., *Munz* 9673 (P). ARIZONA: Chiricahua Mts., *Lemmon* 3073 (G). NEVADA: Big Creek, Lander Co., *Kennedy* 4048 (S). UTAH: Alta, Wasatch Mts., *Jones* in 1879 (P); Marysvale, *Jones* 5384 (P); Red Butte, *Clemens* in 1908 (S); Salt Lake City, *Watson* 769 (G). IDAHO: Deer Lake, Washington Co., *Jones* in 1899 (P); Silver City, Owyhee Co., *Macbride* 929 (P,S); Pocatello, Bannock Co., *Pennell* in 1915 (S); Moscow, Latah Co., *Abrams* 540 (P,S); Coeur d'Alene Lake, *Jones* in 1905 (P); west of Ashton, Fremont Co., *Pennell* 6051 (G). MONTANA: Big Fork, Flathead Lake, *Clemens* in 1908 (G,S), *Jones* 8908 (P); Bozeman, *Scribner* 182 (G), *Moore* in 1901 (P,S); Spanish Creek, Gallatin Co., *Vogel* in 1901 (G). WYOMING: Halleck Canyon, Albany Co., *Nelson* 7430 (P); Newcastle, *Bates* in 1896 (G); 12 miles north of Evanston, Uinta Co., *Pennell* 5911 (G,S); hills east of Afton, Lincoln Co., *Payson & Armstrong* 3247 (P). COLORADO: Larimer Co., *Baker* 7932 (P); Boulder, *Vestal* 343 (S); Wolhurst, Douglas Co., *Duthie & Clokey* 3860 (G,P,S); Sulphur Springs, Grand Co., *Osterhout* 3233 (G,S); near Golden, *Jones* 250 (P), *Pennell* 5818 (G); Chicken Creek, West La Plata Mts., *Baker, Earle, Tracy* 820 (P). SOUTH DAKOTA: Elk Canyon, Black Hills, *Rydberg* 913 (G). MICHIGAN: Hancock, *Robbins* 160 (G).

The *C. tenella* of Piper (Contr. U.S. Nat. Herb. 11:496. 1906) is based on *Antirrhinum tenellum* Pursh Fl. 2:421. 1814. PURSH'S description is based on a collection made by *Lewis* on the LEWIS and CLARK Expedition. PURSH states that the plant was found "on the banks of the Missouri" in July. In the Academy of Natural Sci-

[1] Such herbarium sheets have been selected for citation from those studied as will give some indication of range.

ences at Philadelphia there is a specimen of *C. parviflora* collected on April 19, 1806 at Rockford Camp. This plant was discussed by Meehan (Proc. Philad. Acad. **50**:12–49. 1898) who reported identifications made by ROBINSON and GREENMAN. They considered it as representing *Antirrhinum tenellum* Pursh, and, according to the data with the specimen, from Rockford Camp, at the mouth of Mill Creek, near the Dalles, Ore. Dr. PENNELL has kindly examined this specimen for me and writes that it disagrees with PURSH's description in having the stem branched and pubescent, the flowers long-pediceled and doubtless small, although they have been lost from the specimen. He suggests that it is very doubtful whether this specimen represents *Antirrhinum tenellum* Pursh, although he has no other plant to suggest. Because of this uncertainty with regard to the species name *tenella*, it seems better to maintain *parviflora*, for which species there is authentic material, even though the former name has been used in many recent manuals (Coulter & Nelson, Rocky Mt. Manual, 439. 1909; Britton & Brown, Fl. No. Sts. & Can. **3**:189. 1913, ed. 2; Wooton & Standley, Contr. U.S. Nat. Herb. **19**:579. 1915; Tidestrom, Contr. U.S. Nat. Herb. **25**:485. 1925).

With such a large geographical range, since *parviflora* is by far the most widespread of all the species of *Collinsia*, one would expect that there would be several differences found worthy of varietal rank. The most noteworthy variations are as follows: (1) the more slender habit of the Canadian plants; (2) the somewhat thickened leaves of plants from the southern part of Idaho and Utah, and (3) broad-leaved forms from Montana. But such indefinite and minor variations seem unworthy of nomenclatural recognition. This species is distinct from *grandiflora* var. *pusilla*, which it resembles, in corolla length and in the possession of an almost erect and gibbous corolla tube in contrast to a declined and saccate tube. In studying these two closely allied species, one finds a continuous series of intergradation from the largest-flowered *grandiflora* var. *typica* through *grandiflora* var. *pusilla*, to the smallest-flowered *parviflora*, and yet the two extremes differ greatly. The saccate tube of *grandiflora* gradually gives way to the gibbous tube of *parviflora* or vice versa, and so with the other changing characteristics. Some material

from southeastern Washington and adjacent parts of Idaho is rather hard to place, for the flowers have the characteristics of rather small-flowered *grandiflora* var. *pusilla*, but occur in regions where *parviflora* also is found, and would ordinarily be taken for *parviflora* (Pullman, Wash., *Elmer* 162.-P). On careful examination, however, it is found that the corollas of these specimens are declined and saccate. After considering also the length of the corolla I have placed them in *grandiflora* var. *pusilla*. I have included some doubtful material collected by *Lemmon* (3073) from the Chiricahua Mts. in Arizona. It is not at all typical, for the corolla throat is open, the upper lip not at all reflexed, the tube slender and not gibbous, and the plant quite conspicuously glandular. Additional material from the same locality is desirable. The only other Arizona collection seen (Prescott, *Palmer* 635, *G*) is quite typical.

13. COLLINSIA GRANDIFLORA Dougl. in Lindl., Bot. Reg. **14**: *t.* 1107. 1827; Hooker Fl. Bor. Am. **2**:94. 1838.

Stems erect, simple, branching, or rarely somewhat decumbent, glandular-pubescent above to glabrate below, 5–40 cm. tall; leaves oblong to lanceolate, becoming linear in upper whorls, obtuse to acute, sessile or occasionally very slightly petiolate, glabrate, serrulate to entire or entire-revolute, scabrous-margined, 1–4 cm. long, 0.3–1.3 cm. wide becoming smaller and bractiform in inflorescence; lower leaves oblong to spatulate, obtuse, with petioles 5–10 mm. long; flowers 3–7 at a node, rarely solitary; pedicels puberulent, inconspicuously glandular, 0.3–2 cm. long; calyx membranous below, glabrate-puberulent, scabrous-margined, 4–7 mm. long; calyx lobes subulate, acuminate, 2–5 mm. long, 1–1.5 mm. wide; corolla strongly declined, 7–15 mm. long, forming a right angle with the pedicel, upper lip white to purple, lower lip deep blue-violet, lips reflexed about half the corolla length; corolla tube 3–5 mm. long, 2–4 mm. wide; dorsal saccate region deep at base, somewhat declined toward mouth of tube, sparsely bearded or glabrous, 1.5–3 mm. deep; upper lip 3–6 mm. long, sinus 1–4 mm. deep; upper lobes recurved from narrow callous ridge of upper lip, obovate, retuse-entire, 2–4 mm. wide; lower lip 4–9 mm. long; keel 1.5–3 mm. deep, ca. 1 mm. shorter than lateral lobes; lateral lobes obovate, emarginate-retuse, occasionally entire, 2–5.5 mm. wide; filaments rather stout, glabrous,

the upper pair often bearded at lowest attachment point; stigma two-lobed, but not always plainly so; capsule 4–5 mm. long, exceeded only by calyx tips; seeds normally 4, thickened, round-oblong, smooth, reddish-brown when mature.

**Key to varieties**

A. Corolla 7–9 mm. long; lobes reflexed ½–⅓ the corolla length
13*a*. *C. grandiflora* var. *pusilla*

A. Corolla over 10 mm. long, broad lobes reflexed about ½ the corolla length.....13*b*. *C. grandiflora* var. *typica*

13*a*. C. GRANDIFLORA var. PUSILLA Gray Syn. Fl. No. Am. **2**:256. 1878; Jepson Man. Calif., 904. 1925; *C. pusilla* Howell Fl. N.W. Amer. **1**:506. 1901; *C. multiflora* Howell Fl. N.W. Amer. **1**:506. 1901; *C. parviflora* var. *minima* (Nutt.) Jones, Contr. West. Bot. **12**:69. 1908.

Corolla 7–9 mm. long, tube saccate at base; corolla lobes rather broad, reflexed one-half to one-third the total corolla length.

**Type locality.**—"Plumas Co., California."

**Specimens studied.**—BRITISH COLUMBIA: Vancouver Is., Victoria, *Macoun* 718, 719, 720 (G), Nanaimo, *Fowler* 8 (G), Oak Bay, Victoria, *Pineo* in 1901 (P). WASHINGTON: Puget Sound, *Cooper* (G); Olympic Mts., Clallam Co., *Elmer* 2586 (P,S); Sequim, *Grant* in 1916 (S), *Grant* 234 (G); Langley, *Grant* in 1922 (G); Pullman, *Elmer* 162, type of *parviflora* var. *minima* (P 14470, 45049); Hangman Creek, Spokane Co., *Sandberg & Leiberg* in 1893 (G,P). OREGON: Willamette Heights, Portland, *Sheldon* 10308 (G,P,S); Orcas Is., *Lyall* in 1858 (G); west of Salem, *Nelson* 2038 (G); Roseburg, *Howell* in 1881 (S); The Dalles, *Lunell* in 1903 (G,S); near Lexington, Morrow Co., *Leiberg* 17 (G); near Harper Ranch, Mathew Co., *Leiberg* 2085 (G). CALIFORNIA: without locality, *Rattan* in 1883 (S); Plumas Co., *Mrs. Austin* without data, type collection (G). IDAHO: Hatwai Creek, Nez Perces Co., *Sandberg, McDougal, Heller* 38 (G,S).

This variety is characterized by the rather small size of the corolla and the narrower and shorter corolla lobes.

13*b*. C. GRANDIFLORA var. **typica,** nom. nov.—*C. grandiflora* Dougl. in Lindl., Bot. Reg. **14**:*t.* 1107. 1827; Hooker Fl. Bor. Am. **2**:94. 1838; Benth. in DC. Prodr. **10**:318. 1846; Gray Syn. Fl. No. Am. **2**:256. 1878; Jepson Man. Calif., 904. 1925; *C. Diehlii* Jones, Contr. West. Bot. **12**:68. 1908.

Corolla 10–15 mm. long, the tube saccate at base; corolla lobes broad, retuse, reflexed half the total corolla length.

**Type locality.**—"Dry gravelly banks of the Columbia."

**Material studied.**—BRITISH COLUMBIA: Vancouver Is., *Wood* in 1859–60 (G). WASHINGTON: Mt. Hamilton, *Gorman* 4588 (S); Steilacoom, *Cooper* (G); near Lower Cascades, *Suksdorf* in 1886 (G); Bingen, Klickitat Co., *Suksdorf* 184 (S). OREGON: Portland, *Jones* in 1902 (P); Oregon City, *I. E. Diehl* in 1902, type of *Diehlii* (P); Salem, *Nelson* 1065, 1177 (G); Forest Grove, *Henderson* in 1883 (G); Grant's Pass, *Henderson* 1379 (G); Multnomah Co., *Howell* 263 (G), La Turelle Falls, *Sheldon* 11910 in 1903 (S). CALIFORNIA: Quartz Valley, Siskiyou Co., *Butler* 1226 (P); Redwood Belt, Humboldt Co., *Chandler* 1251 (S); Mong Valley, Mendocino Co., *Bolander* 4675 (G); Sierra Valley, Big Meadows, *Lemmon* in 1879 (G).

This variety is quite distinct with its large flowers and broad reflexed lobes. There is great variation in the size of plants but this has little significance taxonomically.

14. COLLINSIA RATTANII Gray, Proc. Am. Acad. **15**:50. 1880.

Plant 10–40 cm. tall; stems much branched, or occasionally simple, puberulent-glabrate below, glandular-pubescent above, giving a dull hue to plant; leaves thickened, gray-green, often purplish below, linear-elongate, entire and revolute to serrulate, obtuse, glabrous, 1–6 cm. long, 2–6 mm. wide, becoming gradually reduced in inflorescence to small linear bracts 2–5 mm. long in uppermost whorls; basal leaves much shorter, ovate to oblong, with petioles 5–10 mm. long; flowers 1–4 at a node; pedicels conspicuously glandular-pubescent, 3–10 mm. long; calyx one-third to two-thirds the length of corolla, glandular-pubescent, cleft half its length, 2.5–5 mm. long; calyx lobes deltoid-lanceolate, acute, 1–2.5 mm. long; corolla gibbously declined to erect, light blue to violet, 5–14 mm. long; corolla tube 2–5 mm. long, 1.5–4 mm. wide; dorsal saccate region 1–2.5 mm. deep, sparsely short-bearded within; upper lip 2.5–11 mm. long, one-third to two-thirds of its length reflexed; upper lobes ovate-oblong, retuse-entire, sinus 1–3 mm. deep; lower lip 2–11.5 mm. long; keel as long as or ca. 1 mm. shorter than lateral lobes, 1–3 mm. deep, often sparsely bearded without; lateral lobes ovate to spatulate, retuse-entire, 1–5.5 mm. wide; lateral saccate region bearded; upper filaments bearded at basal attachment, often with a rudimentary bearded appendage ca. 0.3 mm. long; stigma not lobed; capsule 4–5 mm. long, equaled by calyx lobes; seeds somewhat flattened, slightly margined, oblong, 1.5–2 mm. long, 2–6 in number.

**Key to varieties**

A. Corolla less than 7 mm. long, appearing tubular, lobes inconspicuous; corolla lips no longer than tube

14*a*. *C. rattanii* var. *typica*

A. Corolla over 7 mm. long, lobes reflexed, conspicuous; corolla lips longer than to twice as long as the tube

14*b*. *C. rattanii* var. *linearis*

14*a*. C. RATTANII var. **typica,** nom. nov.—*C. rattanii* Gray, Proc. Am. Acad. **15**:50. 1880; Syn. Fl. No. Am. **2**:439 (supplement). 1886; *C. glandulosa* Howell Fl. N.W. Amer. **1**:506. 1901; *C. torreyi* var. *rattanii* Jepson Man. Calif., 905. 1925.

Corolla less than 7 mm. long, tubular; corolla lobes inconspicuous, usually not as long as the tube.

**Type locality.**—Open hillsides south of Trinity River, California.

**Specimens studied.**—WASHINGTON: West Klickitat Co., *Suksdorf* in 1886 (G); White Salmon, *Suksdorf* 301 (G). OREGON: Currant Creek, *Howell* 507 (G); The Dalles, *Howell* in 1882 (S); Cold Camp, John Day Valley, (photograph) *Howell* in 1885, type of *glandulosa* (G); state line between California and Oregon, *Diehl* 129 (P). CALIFORNIA: Siskiyou Co., Quartz Valley, *Butler* 609 (P), Klamath River, *Butler* 1188 (P,S); Black Butte, *Rattan* in 1884 (S); south of Trinity River, *Rattan* in 1879, type collection (G); Trinity and Humboldt Cos., *Rattan* in 1883 (G); near Bennett Spring, Glenn Co., *Heller* 11949 (S); Mt. Sanhedrin, Lake Co., *Eastwood* in 1925 (P), *Rattan* in 1884 (G,S).

There is much variation in the vegetative forms of this species, but in the corolla is found a definite intergradation with respect to size and shape. This corolla series is so marked that *linearis* is now recognized as only a variety of *rattanii*. Indeed, GRAY seems to have had difficulty too, for a specimen collected by *Greene*, 742*a*, in 1876 (G), is cited by GRAY as *rattanii* in the original description of that species. The same specimen is cited as *linearis* in Syn. Fl. N. America, supplement, **2**:439. 1886. The specimen is decidedly on the borderline between the two varieties, but because of the size of the corolla, it is here placed with *linearis*. *Typica* is characterized by the small, tubular corolla with short, inconspicuous lobes. The *rattanii* group is separated from the *torreyi* group, with which JEPSON confused it, by the presence of bracts in the upper whorls of the inflorescence.

14*b*. C. RATTANII var. **linearis** (Gray), comb. nov.—*C. linearis* Gray, Proc. Am. Acad. **15**:50. 1880; Syn. Fl. No. Am. **2**:439 (supplement). 1886; *C. torreyi* var. *linearis* Jepson Man. Calif., 905. 1925.

Corolla over 7 mm. long, lobes reflexed and conspicuous; corolla lips longer than to twice as long as the tube.

**Type locality.**—Along Klamath and Trinity rivers, on argillaceous-rocky hills, N.W. California.

**Specimens studied.**—OREGON: Waldo, *Rattan* in 1879 (G), *Howell* 229 (G,S); Siskiyou Mts., Jackson Co., *Abrams & Benson* 10199 (S); between Grove and Wolf creeks, Josephine Co., *Abrams & Benson* 10433 (S); Grant's Pass, *Heller* 10020 (S), *Dale* in 1913 (S); Gerlinger, Polk Co., *Nelson* 2070 (G). CALIFORNIA: without locality, *Greene* 742*a* (G); near Yreka, *Greene* 742 (G); Humbug Mt., Siskiyou Co., *Butler* 1262 (P,S), *Butler* 758 (P); Shasta Retreat, *Heller* 7946 (S); south of Trinity River, *Rattan* 21 (G); along Klamath and Trinity rivers, *Rattan* 54, in 1879, type collection (G); Hoopa Valley, Humboldt Co., *Rattan* in 1878 (S), *Chandler* 1294 (S).

This variety has much variation in corolla size in specimens from a given locality, as from Waldo, Oregon (*Howell; Rattan*) and Grant's Pass (*Dale; Heller*), but the increase in corolla size and the broader and more conspicuous corolla lobes make it distinct from *typica*.

15. COLLINSIA CHILDII Parry, in Gray Syn. Fl. No. Am. **2**:257. 1878; Jepson Man. Calif., 905. 1925; *C. inconspicua* Congdon, Erythea **7**:187. 1900; *C. breviflora* Suksdorf, West. Am. Sci. **12**:54. 1901.

Plant erect, much branched, glabrate to puberulent below, glandular-pubescent above, 10–40 cm. tall; leaves serrulate to entire-revolute, scabrous-margined, glabrous, ovate-rotund to oblong or lanceolate, obtuse-acute, 1–5 cm. long, 0.5–1.5 cm. wide; lower leaf petioles not over 1 cm. long; flowers 2–4 at a node, occasionally 1–5; pedicels glandular-puberulent, 0.5–1 (–2) cm. long, the lower subtended by leaves, the upper by oblong-linear bracts less than 1 cm. long; calyx scarious, each lobe with 1–3 darker green veins, glandular-pubescent, 4–7 mm. long; calyx lobes broadly lanceolate, narrowly obtuse to acute, 2–4 mm. long; corolla lavender to white, region below the sinus of upper lip purple-spotted, 6–8 mm. long; corolla tube 3–4 mm. long, 1.5–2.5 mm. wide; dorsal gibbous region shallow,

ca. 0.5 mm. deep, usually with short gland-bearding at the base; upper lip 2–2.5 mm. long, the sinus 1–1.5 mm. deep; upper lobes broadly obtuse, ca. 1.5 mm. wide; lower lip 2–3 mm. long; keel ca. 1 mm. shorter than lateral lobes, 1 mm. deep, often gland-bearded without; lateral lobes spatulate, 1–1.5 mm. wide; lateral sac occasionally sparsely gland-bearded; filaments glabrous; stigma not lobed; capsule 3–4 mm. long, exceeded by calyx lobes; seeds 2, thick, round-oblong, ca. 3 mm. long.

**Type locality.**—"South-eastern California, in deep woods in the San Bernardino Mts."

**Specimens studied.**—CALIFORNIA: along Truckee River, Placer Co., *Sonne* 252 (S); Mariposa Co., Putman Mt., *Congdon* 77 (G); Hegan Mt., *Congdon* 61, type of *inconspicua* (G); Tassajara Hot Springs, Monterey Co., *Elmer* 3362 (S); San Rafael Mts., *Ford* in 1887 (G); Pine Ridge, Fresno Co., *Hall & Chandler* 86, type of *breviflora* (S); Greenhorn Range, Kern Co., *Hall & Babcock* 5028 (S); Tehachapi, *Davidson* in 1895 (S); San Antonio Mts., Bear Canyon, *Peirson* 2156 (P); Upper San Sevaine Flats, *Johnston* 5111 (P); San Bernardino Mts., *Parry & Lemmon* 298, probably type collection (G), *Parish* 911 (S); Burnt Mill Ranger Station, *Munz* 8155 (P); Fredalba, *Munz & Williams* 2940 (P); Palomar Mts., *Hall* 1942 (P,S); *Parish* 4407 (G); Cuyamaca Mts., *Brandegee* in 1894 (S); Laguna Mts., *Mearns & Schoenfeldt* in 1894, in part (S); Descanso Creek, San Diego Co., *Munz & McCully* 8098 (P).

Characterized by the broadened, serrulate-entire, thin leaves, and by the calyx, which is membranous at base and exceeds the capsule, *childii* is distinct from all other species.

16. COLLINSIA CALLOSA Parish, Erythea 7:96. 1899; Jepson Man. Calif., 905. 1925.

Plant stout, erect, diffusely branching, glabrous below, glandular-pubescent above, 5–25 cm. high; leaves thickened, succulent, glabrous, purplish below, oblong to ovate, obtuse to acute, entire, margins revolute, not over 3 cm. long, 1 cm. wide; gradually reduced to small linear bracts in upper inflorescence; lower leaves sessile or with petioles 1–4 mm. long; pedicels glandular-pubescent, 0.5–1.5 cm. long, 1–3 at a node; calyx glandular-pubescent to glabrate, 5–7 mm. long, becoming conspicuously broad (5 mm.) at base in fruit; calyx lobes broadly deltoid-lanceolate, acute, 2–3 mm. long, ca. 1 mm. wide in flower, becoming ovate-acute, 2–3 mm. wide in fruit; corolla rose-lavender, 6–10 mm. long; corolla tube yellowish, 3–5

mm. long, ca. 2 mm. wide; dorsal saccate region shallow, ca. 1 mm. deep, short-bearded to glabrous within; upper lip 3–4 cm. long, 2–3 mm. wide, its sinus 1.0–1.5 mm. deep, subtended by a yellow-rose-colored purple-spotted region above the callosity; upper lobes round-obtuse (rarely emarginate), 1.0–1.5 mm. wide; lower lip ca. 0.5 mm. longer than upper lip; keel 1 mm. shorter than lateral lobes, ca. 1 mm. deep; lateral lobes narrowly spatulate, obtuse, ca. 1 mm. wide; lateral sac yellowish, calloused, 2–3 mm. long; filaments pale lavender, glabrous, upper pair rarely sparsely bearded and with a rudimentary bearded basal appendage ca. 0.4 mm. long; anther sacs purple; stigma not lobed; capsule 4–6 mm. long, slightly longer than the calyx lobes; seeds 6, oblong, thickened, rugose-reticulate, ca. 2 mm. long.

**Type locality.**—Swartout Canyon, San Antonio Mts.

**Material studied.**—CALIFORNIA: Panamint Mts., near Willow Creek, *Coville & Funston* 750 (G,S); Millspaugh, Argus Mts., *Hall & Chandler* 7079 (P); Lee District, Nelson Range, *Hall & Chandler* 7149 (P); foothills south of Bishop, *Heller* 8290 (S); Mt. Piños, Cuddy's, *Dudley & Lamb* 4516 (P,S), Seymour Creek, *Munz* 6961 (P); Tehachapi, *Jones* in 1903 (P), Water Canyon, *Abrams & McGregor* 439, in part (S); Lancaster, *Davidson* in 1895 (S); Mt. Gleason, Acton, *Elmer* 4178 (S); San Antonio Mts., *Hall* in 1899, probably type collection (S), Swartout Canyon, *Hall* 1492 (P,S); Big Rock Creek, *Munz* 6803 (P); hills bordering Mojave Desert, *Pringle* in 1882 (G); Crystal Creek, San Bernardino Mts., *Jaeger* in 1927 (P).

*C. callosa* has the appearance of a desert form of *childii*, but with the more numerous and smaller seeds, and the thick, succulent leaves and calyces, it is quite distinctive.

17. COLLINSIA TORREYI Gray, Proc. Am. Acad. **7**:378. 1868.

Stems erect, widely branched, occasionally simple, glandular, very floriferous, 5–20 cm. tall; leaves linear to elliptical, slightly thickened, glabrous, entire to serrulate, 1.5–4.5 cm. long, 0.5–10 mm. wide; lower leaves smaller, spatulate-oblong, with petioles 5–10 mm. long; flowers commonly in 3–6 flowered whorls, occasionally fewer; pedicels glandular, 5–10 mm. long, bracts obsolete or less than 2 mm. long above, to filiform and 5–10 mm. long below; calyx moderately glandular, 2–4 mm. long, cleft for half its length, lobes linear-obtuse, 0.5–1 mm. wide; corolla 4–9 mm. long, gibbously declined, all blue-violet or the upper lip paler or yellowish to white;

corolla tube 2–4 mm. long, 1.5–3 mm. wide, throat broad and open; dorsal gibbous region shallow, less than 1 mm. deep, glabrous or sparsely bearded within near base; upper lip 2–4 mm. long, sinus ca. 1 mm. deep, lobes truncate, 1–2 mm. wide, somewhat reflexed from the callous ridge which has 2 toothlike crests; lower lip 2.5–5 mm. long; keel as long as to ca. 2 mm. shorter than lateral lobes, 1–2 mm. deep; lateral lobes broadly spatulate, obtuse-truncate, 1–2 mm. wide; filaments glabrous or the upper pair bearded at basal attachment, appearing broad; stigma 2-lobed, often inconspicuously so; capsule 2.5–4 mm. long, equaled by calyx lobes; seeds 2, thick, round-oblong, rugulose, 2–2.5 mm. long.

**Key to varieties**

A. Flowers 6–9 mm. long.
  B. Keel as long as lateral lobes, or less than 1 mm. shorter.
    C. Leaves linear, many times as long as wide. Sierra Nevada Mountains.....17*a*. *C. torreyi* var. *typica*
    C. Leaves elliptical or lance-ovate, 2–4 times as long as wide. Northern California, southern Oregon
      17*b*. *C. torreyi* var. *latifolia*
  B. Keel 1–2 mm. shorter than the broad lateral lobes of corolla. Tulare and Fresno counties...17*c*. *C. torreyi* var. *brevicarinata*
A. Flowers less than 6 mm. long; plant 4–20 cm. tall
  17*d*. *C. torreyi* var. *wrightii*

17*a*. C. TORREYI var. **typica,** nom. nov.—*C. torreyi* Gray, Proc. Am. Acad. **7**:378. 1868; Syn. Fl. No. Am. **2**:257. 1878; Jepson Man. Calif., 905. 1925.

Leaves linear, many times as long as wide; flowers 6–9 mm. long, keel as long as lateral corolla lobes or less than 1 mm. shorter.

**Type locality.**—Mariposa Big-tree Grove, California.

**Material studied.**—CALIFORNIA: Grove of large trees (Mariposa Big-tree Grove), *Torrey* in 1865, type collection (G); near Donner Lake, *Torrey* in 1865 (G), *Heller* 6914 (P,S); Emigrant Gap, *Jones* in 1882 (P); Tallac, Lake Tahoe, *Abrams* 7328 (S); Antelope, Amador Co., *Hansen* 4714 (S); Clark's and Yosemite Valley, *Bolander* 4874 (G), vicinity Hog Ranch, *Hall & Babcock* 3393 (P,S), trail from Tioga Road to Yosemite Falls, *Munz* 7521 (P); Hegan Mt., Mariposa Co., *Congdon* in 1894 (S); Huntington Lake, *Grant* 1034 (S); Pine Ridge, Fresno Co., *Hall & Chandler* 61 (S).

*C. torreyi* differs from the other species of the genus in the absence or minuteness of bracts in the upper whorl of the inflorescence. Within the group are several variations worthy of recognition. In *typica* the color of the corolla varies from blue-violet to forms with a paler or even white upper lip (*Munz*, trail from Tioga Road to Yosemite Falls). It is easily recognized by the large flowers (in contrast with those of *wrightii*) and the long linear leaves.

17*b*. C. TORREYI var. **latifolia,** var. nov.

Folia elliptica aut lanceolato-ovata, ca. 2–4 longiora quam lata; floribus 6–9 mm. longis; labio superiore luteo-albo.

**Type,** Ashland Butte, southern Oregon, *Cusick* 2893 (type, Pomona College Herbarium no. 42879; cotype at Gray). **Other material,** OREGON: Ashland Butte, *Howell* in 1887 (S), *Henderson* in 1886 (S); border between Oregon and California, *Henderson* in 1886 (G). CALIFORNIA: Sisson, Siskiyou Co., *Brown* 318 (S); Mts. near Yreka, *Greene* 912 (G); Squaw Creek Ranger Station, *Drew* in 1916 (S); Little Hot Springs, Modoc Co., *M. S. Baker* (P).

The following collection is cited as representing an intergradation between *latifolia* and *typica*.—Dorleska, in Salmon Mts., Trinity Co., Calif., *Hall* 8569 (P,S).

This variety is recognizable by its very broad leaves and its separate geographical range.

17*c*. C. TORREYI var. **brevicarinata,** var. nov.

Flores 6–9 mm. longi; carina quam lobis lateralibus corollae 1–2 mm. breviore; labio superiore luteo-albo.

**Type,** Hockett's Meadow, Tulare County, California, *Culbertson* 4220 (Pomona College Herbarium no. 14844; cotype, Stanford). **Other material,** CALIFORNIA: Hockett's Meadow, Dudley 1899 (S); between Mineral King and Farewell Gap, *Hall & Babcock* 5394 (S); Alta, *Grant* in 1902 (S); vicinity of Homer's Nose, Sequoia Nat'l Forest, *Dudley* 1834 (S); Mt. Silliman, Clover Creek, *Dudley* 1467 (S); near Mineral King, *Coville & Funston* 566 (G); Sierra Nevada Mts., *Grant* 199 (S); Fresno Co., Sequoia Mills, *Eastwood* in 1894 (G); Sequoia Horse Corral Meadow, *Dudley* 3167 (S).

Like *wrightii* in leaf characters, and with the corolla appearing like *typica* at a glance, *brevicarinata* is separated by the conspicuously shortened keel of the broad-lobed flowers.

17*d*. C. TORREYI var. WRIGHTII (Wats.) Johnston, Plant World 22:115. 1919; Jepson Man. Calif., 905. 1925; *C. wrightii* Wats., Proc. Am. Acad. 24:84. 1889; *C. brachysiphon* Eastw., Bull. Torr.

Bot. Club **32**:214. 1905; *C. torreyi* var. *brachysiphon* (Eastw.) Jepson Man. Calif., 905. 1925; *C. monticola* Davidson, Bull. So. Calif. Acad. Sci. **16**:13. 1917.

Plants 4–29 cm. tall; bracts of upper whorls of inflorescence obsolete or minute, except when plants are immature and lower bracts are ca. 1 cm. long and appear as the upper ones; flowers 4–6 mm. long.

**Type locality.**—Greenhorn Mts., Kern Co.

**Material studied.**—NEVADA: Divide south of Slide Mt., Washoe Co., *Heller* 10967 (S). CALIFORNIA: Black Butte, Siskiyou Co., *Rattan* in 1884 (S); Lassen Peak, *Jones* in 1897 (P); above Jonesville, Butte Co., *Heller* 12028 (S); Soda Springs; Nevada Co., *Jones* 2394 (G,P); Cisco, Placer Co., *Heller* 12722 (S), Summit, *Heller* 9855 (S); El Dorado Co., Mt. Tallac, *McGregor* 190 (S); Half Moon Lake, *McGregor* in 1909 (S); near Camp Echo on Lincoln Highway, *Heller* 12173 (S); Webber Lake, *Doten* 65 (S); Tuolumne Co., meadows, *Ware* 2615c, 2630c (G); Yosemite, *Gray* in 1872 (G); Phillips, Tulare Co., *Evans* in 1920 (P), Funston's Meadows, Kaweah Peaks, *Dudley* 2189 (S); Tobias Meadow, Kern River Valley, *Dudley* 622 (S); Greenhorn Mts., Kern Co., *Hall & Babcock* 5045 (S), *Palmer* in 1888 (G); 12 miles from Kernville, *Wright* 4, type collection (G,S); Tehachapi Mts., Brook Canyon, *Dudley* 322 (S); Water Canyon, *Abrams & McGregor* 442, in part (S); Mt. Piños, Ventura Co., *Abrams & McGregor* 233 (S), *Munz* 7034 (P), *Elmer* 4004 (S); San Gabriel Mts., Lytle Creek Canyon, *Hall* 1441 (S); Ice House Canyon, *Parish* 11955 (P,S); Swartout Valley, *Munz* 4644 (P); Bear Valley, San Bernardino Mts., *Munz* 5682 (P); Bluff Lake, *Munz* 8161 (P), *Newsom* in 1926 (P).

*Wrightii* is most variable in growth habit, making it difficult to key. It seems strange to consider the small 1- or 2-flowered plants collected by *Jones* at Lassen Peak in the same variety with the large Greenhorn Range material of *Hall & Babcock*. This is especially true when one notices the conspicuous bracts on the 1- or 2-flowered specimens; but I am considering the Lassen Peak material and some from Webber Lake collected by *Doten* as atypical and aborted, because in all other small material studied, immature plants of *wrightii* appear this way until the last whorls of flowers are fully developed and then show the lack or minuteness of the upper bracts. Specimens collected from Bluff Lake by *Munz* on June 1, 1924, and by *Newsom* on June 28, 1926, show very well the change of habit which would take place in a month's growth. Specimens from Summit, Placer Co. (*Heller*) also show this variation in the presence of bracts.

*C. brachysiphon* Eastw. is here reduced to synonymy, the material described being one of the variable smaller forms of *wrightii* not distinct enough for separate varietal rank.

**Excluded or doubtful species**

*C. tenella* Benth., in DC. Prodr. **10**:593. 1846, equals *Tonella collinsoides* Nutt.

*C. floribunda* (Gray) Greene, Pitt. **1**:55. 1887, equals *Tonella floribunda* Gray.

*C. tricolor* Rafin. Cat. 13. 1824. Probably *C. verna* Nutt. but am unable to get any information concerning it.

*C. barbata* Bosse, Verh. Berl. Gartenb. Ver. N. Reih. **1**:399. 1853, equals *C. tinctoria* Hartw. according to GRAY Syn. Fl. No. Am. **2**:255. 1878.

*C. purpurea* Rafin., Cincinnati Lit. Gaz. 85. 1824; Atl. Jour. 149. 1832. According to RAFINESQUE'S descriptions, *C. purpurea* is much like *C. violacea*, but because of the present range of *violacea*, and due to the fact that no collections of *violacea* have been made east of the Mississippi from the vicinity in which RAFINESQUE states that he found *purpurea*, I feel that what he collected may have been a rather small, unicolored form of *verna*. There is no definite information upon which to base such a decision, however, so *C. purpurea* is placed here rather than in synonymy. *C. purpurea* var. *cuneata* Rafin., *l.c.* and *C. purpurea* var. *parviflora* Rafin., *l.c.* are included in this discussion of *C. purpurea*.

*C. hernandezii* Elmer, BOT. GAZ. **41**:310. 1906. Probably a form of *C. bicolor* var. *typica*, as indicated by description and locality; am unable to locate type material.

POMONA COLLEGE
CLAREMONT, CALIF.

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# STUDIES IN CALIFORNIAN HEPATICAE

## I. ASTERELLA CALIFORNICA

ARTHUR W. HAUPT

(WITH PLATE X AND TWENTY-ONE FIGURES)

Notwithstanding its large number of species of world-wide distribution, *Asterella* has not received the same critical morphological study which has been given to many of the other Marchantiales. The genus belongs to the Rebouliaceae of EVANS (14), a family including four other well known genera, *Plagiochasma* (*Aytonia*), *Grimaldia*, *Cryptomitrium*, and *Reboulia*. The names *Fimbriaria* and *Hypenantron* have been in common use for the genus, but both are antedated by *Asterella*. Of the fifteen North American species described by EVANS (9, 14), four occur in California, the commonest one being *A. californica*. The general structural features of this species, especially those of value in classification, are fully presented by HOWE (15) and EVANS (9), while a number of facts relating to its development are given by CAMPBELL (3).

EVANS (14) gives the distribution of *Asterella californica* as "Arizona, California, and Guadalupe Island." According to HOWE (15) it is found in California, "on open or lightly shaded banks, often about rocks, from San Diego as far north, at least, as Mendocino and Shasta Counties." Some of the material used in the present study was collected along a stream bank in Calaveras County, but most of it came from various canyons in the San Gabriel Mountains of Los Angeles County. *A. californica* is the commonest liverwort in the mountains of southern California, being locally abundant on moist banks and canyon sides during the late fall, winter, and early spring. The plants dry up during the long rainless summer, but, as CAMPBELL (3) says, "the ends of the branches remain alive, so that each growing tip becomes the beginning of a new plant." Soon after the plants are revived by the autumn rains, the production of sex organs begins. The most favorable material for the study of their development was collected in October. Although some individuals

may bear mature spores a month or two earlier, the greatest number of plants with ripe sporophytes was found in April.

Another species of *Asterella*, rather common in the San Gabriel Mountains, is *A. palmeri*. In the fall it is difficult, upon superficial examination, to tell this form from the more abundant *A. californica*, but as development proceeds the two may be easily distinguished. The writer has found only these two species of *Asterella* in southern California. In the present investigation *A. palmeri* was used for a study of the development of the embryo, as it was found more favorable for this phase of the investigation than *A. californica*.

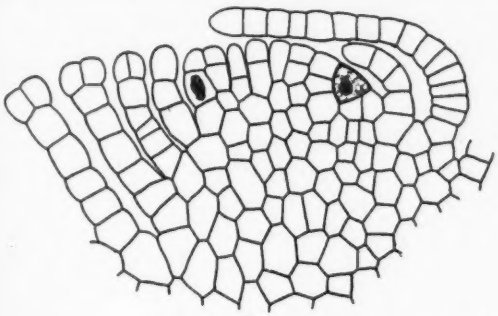

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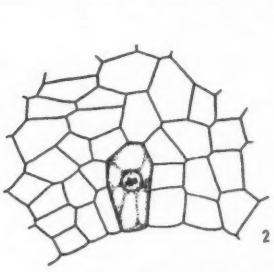
FIG. 1.—Median longitudinal section of sterile thallus, showing apical cell and developing air chambers; ×335.

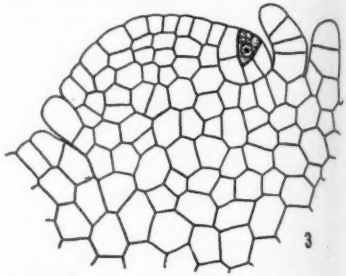
Except for the account of the embryogeny, however, and in a few other places where specifically noted, all statements in this paper refer to *A. californica*.

## THALLUS

The form and structure of the thallus of *Asterella californica* have been accurately described by HOWE (15) and EVANS (9), and most of the facts presented here confirm their observations. The flat, dorsiventral body is green above, but usually slightly purplish below and along the undulate margins. It is rather thick and fleshy, with a conspicuous rounded keel below and on either side, forming a thin wing. There is no dorsal midrib. When dry the margins become strongly incurved. Although some species of *Asterella* produce numerous ventral branches when mature, the branching of *A. cali-*

*fornica* is apparently always dichotomous. The thallus grows by means of a single large apical cell of the cuneate type characteristic of the Marchantiales (figs. 1, 2). Miss PEISSEL (**20**), working on *A. blumeana*, reports that the growing point consists of a transverse row of four cells, of which the "apical cell" seen in median longitudinal section is but one member. A careful study was made of this matter, and while occasionally more than one apical cell seemed to be present, because such cases as shown by fig. 2 were so well defined, it was concluded that there is only one apical cell. When growth is vigorous, the immediate lateral segments of the apical cell are difficult to distinguish from the cell itself.





FIGS. 2, 3.—Fig. 2, apical cell of thallus sectioned in plane parallel with dorsal surface; ×750; fig. 3, median longitudinal section of very young carpocephalum, showing apical cell at forward margin; ×335.

As in all of the Rebouliaceae, the ventral surface bears two rows of appendaged scales, and also both smooth and pegged rhizoids. EVANS (**9**) says that, in *Asterella*, "rhizoid-initials are apparently not present." With this statement the present study does not agree. Well stained preparations of median longitudinal sections through the apical region clearly reveal the presence of very conspicuous rhizoid initials on the ventral surface, among and just back of the scales which protect the growing point. They are striking because of the unusual density of their protoplasm.

The dorsal region of the thallus consists of loose green tissue, and is sharply distinct from the compact, colorless, ventral region. EVANS (**9**) correctly describes the situation as follows:

> Green tissue rather loose, the air chambers in four or five layers in the median portion, those of the dorsal layer higher and larger than the others but

somewhat subdivided by supplementary vertical partitions often reaching nearly or quite to the epidermis; compact tissue occupying from one-fourth to one-third the thickness of the thallus in the median portion, thinning out gradually on the sides and extending about halfway to the margin.

The air chambers arise schizogenously just back of the apical cell, the split starting at the surface of the thallus and proceeding downward (fig. 1), thus agreeing with CAMPBELL's account (3) and that of Miss PEISSEL (20). Only the first one or two layers of cells are involved, the air chamber being deepened, not by further splitting, but by upgrowth of the surrounding tissue, as the presence of mitotic figures in the epidermal and subepidermal cells clearly shows. This centripetal method of splitting was previously described in *Targionia* by DEUTSCH (4), and later confirmed by Miss O'KEEFFE (19). BARNES and LAND (2) found in an undetermined species of *Asterella* (probably *A. echinella*), as well as in a number of other Marchantiales, that the split is hypodermal in origin and progresses upward. EVANS (8) reports that, in *Grimaldia*, "the place where the split first makes its appearance is not always the same"; it may start either at the surface or below the epidermis. In *Reboulia*, HAUPT (11) describes centripetal splitting, while DUPLER (5) states that the splitting arises both internally and superficially, "generally proceeding from both points of origin simultaneously."

BARNES and LAND (2) also find that, in *Asterella*, secondary splittings occur deep within the dorsal region, the smaller chambers thus formed becoming connected with the primary chambers. Since in the present study no evidence was found of intercellular cleavage, except at the surface of the apical region, the writer is inclined to consider the "secondary" air chambers to be merely extensions of the primary ones. As EVANS (8) reports in *Grimaldia*, the deeper chambers have no supplementary partitions. The cells in this part of the thallus are slightly elongated horizontally, their length being about twice their diameter, and chloroplasts are less abundant here than in the cells above. The single-layered epidermis has thin walls, and is provided with chloroplasts. It is often rich in oil droplets, especially near the growing point. As in the other Rebouliaceae, the thallus air pores are simple, while those on the female receptacle are compound (barrel-shaped).

Intracellular fungi live in the thallus, as in most Marchantiales, and in *Asterella californica* are more or less confined to the upper portion of the ventral region. Here the tissue is colorless and compact, the intercellular spaces being small. Below the fungal zone the cells are elongated horizontally, their length being three or four times their width. They have thin cell walls without pits. EVANS (9) says of *A. californica*, "mycorhiza rarely present in the ventral portion." All of the material used in the present study contained fungi.

## RECEPTACLES

While most species of *Asterella* are monoecious, *A. californica* is strictly dioecious. The male receptacle consists of an elongated, median, dorsal disk very slightly raised above the level of the thallus, thus forming a low pad or cushion. If the thallus branches while antheridia are developing, as frequently happens, the receptacle becomes forked; otherwise there is just one growing point behind which antheridia arise in acropetal succession. EVANS (9) notes that the antheridial receptacle of *A. californica* is located at "some distance from the apex." In nearly all of the male plants collected for the present investigation, as well as those observed both under field and cultural conditions, the receptacle begins at the apical notch and in many cases extends the entire length of the thallus. Thus the production of antheridia, after starting, is a continuous process which accompanies apical growth of the thallus. It neither limits vegetative growth nor ordinarily is followed by the formation of a sterile patch, although sometimes there is an intermittent production of antheridia, and then the condition described by EVANS is seen. While LEITGEB (16) regards a male receptacle of the type present in *A. californica* as very primitive, GOEBEL (10) considers it a reduced structure derived from distinctly delimited, well defined receptacles such as *Reboulia* and certain other forms exhibit, and these in turn from stalked receptacles. In *A. palmeri*, which is monoecious, the antheridial receptacle is still less well defined than in *A. californica*.

Each antheridium lies in a pit formed by upgrowth of the tissue surrounding the young antheridium. Mucilage hairs do not arise

within the pit, *Asterella* differing in this respect from *Reboulia*. The top of the antheridial chamber remains open from the beginning. It communicates with the exterior by means of a pore similar to that found on the vegetative portion of the thallus, a feature observed by LEITGEB. The development of the pore margin is also similar to that of the thallus air pores, except that the inner cells do not become so small and pointed.

The female receptacle arises in the apical notch as a small rounded knob, the apical cell being clearly seen at its forward margin (fig. 3). The latter then undergoes two successive dichotomies, thus forming four new growing points. Behind these the archegonia soon appear. As the receptacle becomes conspicuously dome-shaped by intercalary divisions, air chambers appear, and a short stalk is formed with a groove opening anteriorly. Alternating with the archegonia are short rhizoid furrows continuous with the furrow of the receptacle stalk, a feature first noted by LEITGEB. Because in the species which he studied LEITGEB found that the archegonia occur singly, he regarded the female receptacle as a single branch of the thallus, not as a branch system. CAMPBELL has shown, however, that in *A. californica* two or three archegonia are formed in each row in a radial series, and that thus the receptacle is "composite," representing a branch system as in the higher Marchantiales. The same condition has been described by ABRAMS (1) for *Cryptomitrium*.

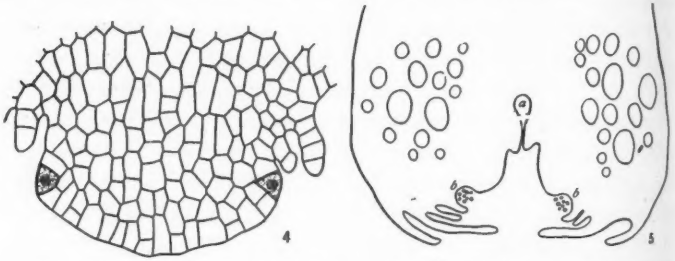
In her recent study, Miss PEISSEL presents an interpretation of the carpocephalum of *Asterella* and related forms not in agreement with that of other investigators, claiming that it arises as a dorsal upgrowth of the thallus, the original apical meristem not undergoing division in connection with its formation. Instead, the meristem remains at the base of the young receptacle, and finally becomes lost in the formation of the stalk.

The mature female receptacle is nearly hemispherical. It is always deeply lobed, the lobes being mostly four in number, frequently five, and rarely six. As a rule only one sporophyte matures under each lobe. The receptacle stalk reaches a length of 10–30 mm., and has but one rhizoid furrow.

## FURTHER GROWTH OF THALLUS

Concerning the relation of the formation of a carpocephalum to further growth of the thallus, EVANS (9) writes:

> The peduncle arises from the apex of a branch, the growth of which is almost invariably brought to an end. . . . . LEITGEB mentions a single specimen of *A. ludwigii* (*Fimbriaria pilosa*) in which an abortive female receptacle failed to limit the growth of a branch, and makes the deduction that such limitation must therefore be a secondary, rather than a primary, result of the development of the receptacle and that the latter is dorsal in origin. No examples of this kind have come to the attention of the writer, but the remarkable conditions sometimes found in *A. californica* may be noted in this connection. In this species,




FIGS. 4, 5.—Fig. 4, section of young carpocephalum cut in plane parallel with dorsal surface of thallus, two apical cells evident; ×335; fig. 5, section of apical portion of young female plant below carpocephalum, cut parallel with surface of thallus: *a*, groove of receptacle stalk; *b*, growing points; ×35.

> as figures by HOWE clearly show, the receptacle may grow out from the bottom of a dichotomy, an ordinary branch appearing on each side. This would seem to indicate a dorsal origin, the apical region of the branch continuing its growth but undergoing a dichotomy at once. The subject, however, deserves further study.

While there is reason to believe that this condition is rare in some parts of California, in the southern part of the state it is rather common, and when plants are grown in a moist chamber a number of carpocephala may be produced on the same thallus, especially if fertilization does not take place.

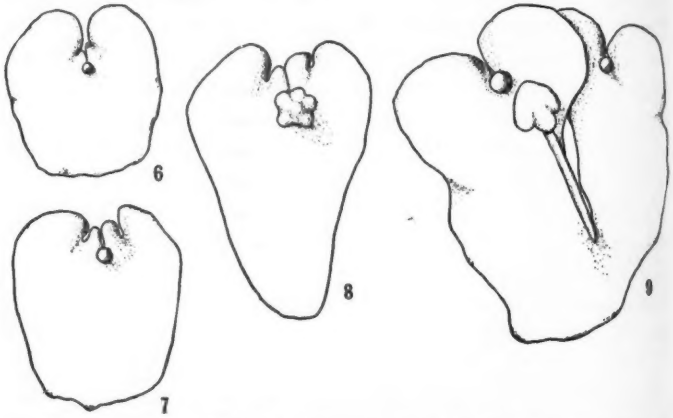
The view that the female receptacle has a dorsal origin is untenable because the apical cell of the thallus is involved in its formation. As already pointed out, CAMPBELL (3) has shown that four (or occasionally five or six) growing points are organized on the

young carpocephalum, each of which gives rise to two or three archegonia in a radial series. The presence of these growing points has been confirmed by the present investigation, and their origin from the primary apical cell of the thallus traced. Fig. 3 shows a single apical cell at the anterior edge of a carpocephalum which is just forming, while fig. 4, cut in a plane parallel with the surface of the thallus, represents a slightly older receptacle in which two apical cells are present. A number of similar stages have been observed. This means that the female receptacle of *Asterella californica* is terminal in origin, and not dorsal as in *Clevea* and *Plagiochasma*. Because the carpocephalum represents a definite branch system, continued growth of the thallus through the activity of the original apical cell is not possible, whereas in cases where it arises as a dorsal upgrowth, the apical cell may continue to function in the usual way.

In forms in which the female receptacle represents a branch system, continued elongation of the thallus may take place by the formation of apical innovations, as in *Preissia* and in certain species of *Asterella;* that is, a single ventral branch may grow out from beneath the receptacle, broadening abruptly and giving the thallus a jointed appearance. In *A. californica*, however, this does not occur. Instead, two new growing points may be organized in the apical notch beneath and just in front of the young carpocephalum (figs. 5–9). As the two lateral branches develop, the receptacle then appears to "grow out from the bottom of a dichotomy," but it should be noted that the receptacle appears before the dichotomy is formed. Each of the branches may again soon give rise to a new receptacle, and the behavior described may be repeated several times. Sometimes one branch becomes suppressed while the other continues to grow, thus giving the thallus an asymmetrical appearance.

It is difficult to determine what factors are responsible for this continued growth of the thallus after a female receptacle has arisen. When plants are grown over the summer in a moist chamber (the period when normally they are dormant in the field) vigorous growth continues, and both male and female receptacles are formed in abundance. The archegonia mature but the antheridia do not, and so fertilization fails to occur. No sperms are discharged from the antheridia of plants grown in a culture chamber, except during the

autumn and winter, which is the time when they mature in the field. When fertilization fails, vegetative growth of the thallus nearly always continues, and the same thing happens when a young female receptacle is excised. Failure of fertilization, then, may stimulate the production of new growing points. It has been observed, however, that sometimes the two new meristems are organized before the archegonia are ripe, and that in the field, as well as under cultural conditions, new receptacles may be formed after sporophytes have developed in the old one.

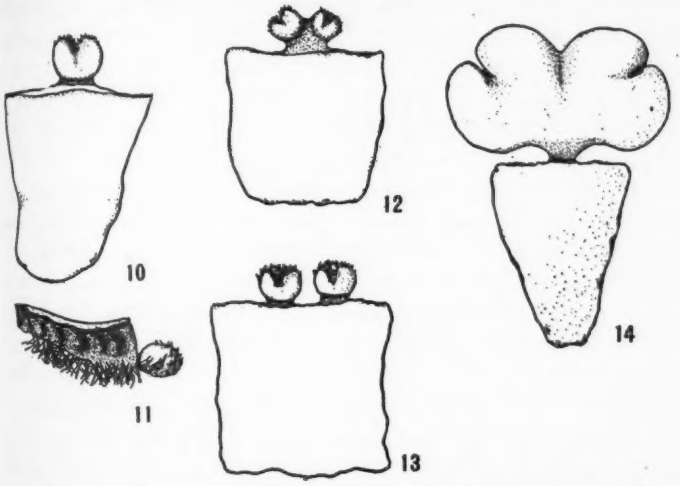



FIGS. 6–9.—Series showing dichotomous branching and continued growth of thallus following the appearance of young carpocephalum; ×3.

The present study has furnished evidence in support of the view that the two growing points arising below and in front of the young female receptacle are adventitious in origin, and bear no relation to the original apical cell of the thallus. Young female plants were sectioned longitudinally, transversely, and in a plane parallel to the surface of the thallus, and in the youngest stages careful examination gave no indication of the presence of one or more apical cells except on the receptacle itself. Thus it seems probable that the two growing points which continue the growth of the thallus arise adventitiously at the posterior inner margin of the wings, and just in front of the groove in the receptacle stalk. A large number of stages

similar to that shown in fig. 5 were seen, but in earlier stages no growing points were evident.

Regeneration experiments were performed to determine whether it is possible for new meristems to be organized after the primary apical cell has been removed. Plants were cut transversely a short distance behind the apical region, and the anterior portion was removed. In nearly all cases new growing points made their appear-




FIGS. 10–14.—Regeneration following removal of apical portion of thallus (fig. 11 is side view of fig. 10, fig. 14 is older stage); ×3.

ance within approximately two weeks. The regenerated portion arises from the extreme ventral region of the thallus, and may consist of one growing point or of two (figs. 10–14). Because the formation of adventitious growing points in these experiments is proved, their organization on the uninjured thallus following the utilization of the primary apical cell by the receptacle is rendered probable.

## ANTHERIDIUM

So far as the writer has observed, the antheridia develop from segments of the apical cell in strict acropetal succession. The superficial, papillate initial (fig. 22) gives rise to a basal and an outer cell,

the former remaining imbedded in the thallus (fig. 23). As a rule the outer cell gives rise to a filament of four cells by the appearance of three additional transverse walls, the sequence of which was not apparent (figs. 24–26). Vertical walls then appear in two planes at right angles to each other; usually, but not always, they arise first in the lower or middle tiers (fig. 27). Commonly additional transverse divisions follow the appearance of the first vertical walls, and result in the formation of five or six tiers of cells (figs. 28–32). At this point, or slightly earlier, the imbedded basal cell divides, either by a transverse or a vertical wall. This account agrees exactly with that described by the writer for *Reboulia* (11) and *Preissia* (13). In both papers, but especially in the latter, a summary of the literature relating to this phase of the life history is given.

Deviations from the usual sequence of wall formation are uncommon. In rare cases vertical walls may appear when the superficial portion of the antheridium consists of only three cells (fig. 34), or there may be five cells before any vertical divisions have taken place (fig. 35). Although CAMPBELL states that, in an undetermined species of *Asterella* (probably *A. bolanderi*), four or five transverse divisions may be formed before the first vertical walls appear, his figures show only three transverse walls in the superficial portion of the young antheridium (the portion derived from the outer cell). This is the normal situation. DUPLER (6) has demonstrated in *Reboulia*, however, that occasionally four transverse walls are formed in the outer cell at this stage of development.

As a rule the spermatogenous tissue is derived from the three upper tiers of cells in the usual way by the formation of periclinal walls (fig. 33), the lower portion of the antheridium forming the stalk. *Asterella* is similar in this respect to *Reboulia* (11), and to both *Preissia* and *Marchantia* (13). CAMPBELL says that periclinal wall formation in *Asterella* is "exactly as in *Riccia*," where he describes the terminal segments as remaining sterile. Other similar cases are mentioned in the *Preissia* paper (13). CAMPBELL also finds that the top of the mature antheridium is prolonged into a beak or tubular neck. This may happen in some cases, but is certainly not the rule.

## Archegonium

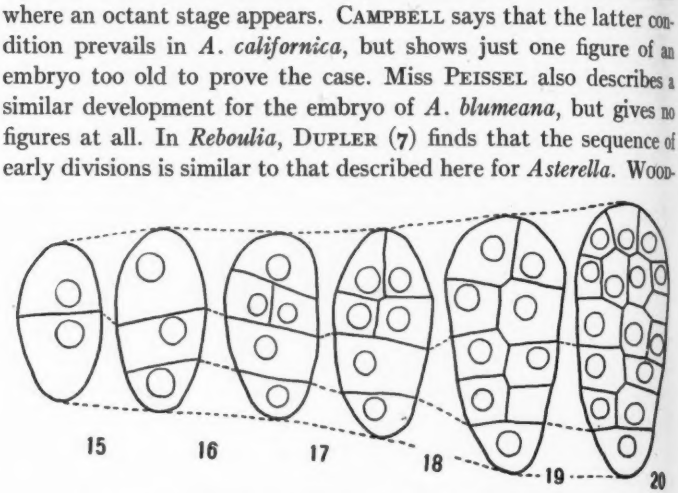
The development of the archegonium is essentially similar to that described by the writer for *Reboulia* and *Preissia*. The earliest stages were not seen. In the youngest stage observed, the primary axial cell and primary wall cells were differentiated, and the basal cell had undergone a transverse division (fig. 36). Further development is typical, the primary axial cell giving rise to the cover cell and central cell (fig. 37), and the latter to the primary neck canal cell and ventral cell (fig. 38). The primary neck canal cell, by two successive divisions, gives rise to four neck canal cells (figs. 39, 40), and then the ventral cell divides to form the ventral canal cell and egg (fig. 41). The cover cell does not divide by a vertical wall until two neck canal cells are formed.

Two cases were seen in which, following the division of the central cell, one of the four neck canal cells had again divided, and in a third instance all of them had divided (fig. 42). Campbell figures an archegonium of *Asterella californica* with an egg, a ventral canal cell, and seven neck canal cells. Thus it seems probable that regularly eight neck canal cells are formed, but that only four are present when the ventral canal cell and egg are differentiated. In *Reboulia* the writer has reported that the number of neck canal cells may later be increased to eighteen or twenty. In *A. palmeri* the central cell divides after four neck canal cells are formed, but no later stages were seen. Variations from the normal development of the archegonium, as found in other Marchantiales, have been mentioned in the *Preissia* paper.

## Embryo

The following account of embryogeny is based on *Asterella palmeri*, as stages illustrating this phase of the life history of *A. californica* were not available. The first division of the fertilized egg is transverse, resulting in two segments approximately equal in size (fig. 15). Two additional transverse walls then appear. In the absence of mitotic figures, their exact sequence could not be established, but it seems likely that a wall appears in each of the two segments. In fig. 16 the hypobasal cell has divided, in fig. 17 the

epibasal cell also. Thus the young embryo consists of a filament of four cells. In this respect *Asterella* resembles *Reboulia* and *Plagiochasma*, but differs from *Preissia*,[1] *Marchantia*, and other forms where an octant stage appears. CAMPBELL says that the latter condition prevails in *A. californica*, but shows just one figure of an embryo too old to prove the case. Miss PEISSEL also describes a similar development for the embryo of *A. blumeana*, but gives no figures at all. In *Reboulia*, DUPLER (7) finds that the sequence of early divisions is similar to that described here for *Asterella*. WOODBURN (21) and HAUPT (12) had previously reported a slightly different sequence, but all three investigators agree that the early embryo consists of a filament of four cells.




FIGS. 15–20.—Stages in development of embryo of *A. palmeri*; ×500

Vertical walls intersecting each other at right angles now appear. In *Reboulia* these begin in the lower tiers, but in *Asterella* they seem to start in the upper ones (figs. 17–19). Additional walls are then formed in the upper part of the embryo (figs. 20, 21), the part destined to become the capsule. It is very difficult, perhaps impossible, to relate the early divisions of the embryo to the ultimate differentiation of the sporophyte into foot, seta, and capsule. The writer's study of *Reboulia*, as well as that of WOODBURN, seems to indicate that the foot arises from the hypobasal segment, the seta and capsule

[1] In the writer's paper on *Preissia*, the literature dealing with the embryogeny of the Marchantiales is presented, but mention of MEYER'S (17, 18) important studies on *Plagiochasma* and *Preissia* was unintentionally omitted.

from the epibasal. DUPLER (7) is led to believe, however, that both the foot and seta come from the hypobasal cell and just the capsule from the epibasal cell. His interpretation is based on substantial evidence, and may be correct. In *Asterella*, the series of stages presented suggests a similar condition. In certain other Marchantiales it has also been shown that the first division of the fertilized egg separates the capsular portion from the rest of the sporophyte.

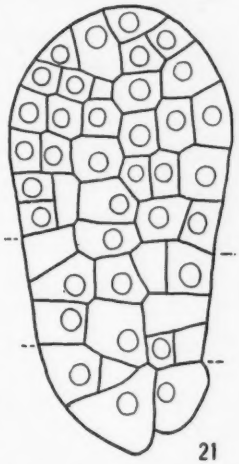



FIG. 21.—Older embryo; ×500.

### OLDER SPOROPHYTE

The mature sporophyte and associated structures have been so adequately described by EVANS (9), that little needs to be said in this place. The capsule is nearly spherical, the seta very short, and the foot bulbous. As in all of the Rebouliaceae, the capsule wall consists of a single layer of cells without annular thickenings. In addition to the involucre, a perianth is developed. *Asterella* is the only genus of the Rebouliaceae having this feature. CAMPBELL has studied the development of the spores and elaters, and also spore germination.

## Summary

1. *Asterella californica*, the commonest species in California, served as the basis for the present investigation, but was supplemented in part by observations on *A. palmeri*.

2. The fleshy, dichotomous thallus grows by means of a single, large cuneate apical cell. The ventral surface bears two rows of appendaged scales, and both smooth and pegged rhizoids.

3. The green tissue is loose and extensive. The air chambers, lacking chlorophyllose filaments, arise schizogenously, the split starting at the surface of the thallus.

4. The air pores are simple on the thallus and male receptacle, and barrel-shaped on the female receptacle.

5. The male receptacle represents a simple dorsal upgrowth of the thallus, the female receptacle a definite branch system, the apical cell of the thallus being involved in its formation. Most commonly four growing points are organized on the latter, and later four conspicuous lobes develop. Ordinarily two or three archegonia arise in each group.

6. Following the formation of a young carpocephalum, a new growing point may appear beneath it at the posterior inner margin of each wing and just in front of the groove in the receptacle stalk. These continue the vegetative growth of the thallus, the receptacle thus appearing to arise from the bottom of a dichotomy.

7. Evidence is presented suggesting that these growing points are adventitious in origin and bear no relation to the original apical cell of the thallus.

8. The development of the antheridium is essentially similar to that of other Marchantiales. Several deviations from the normal sequence of early wall formation are described.

9. Early development of the archegonium presents no unusual features. The ventral canal cell and egg are differentiated after four neck canal cells are formed, but this number is then increased to eight.

10. Before any vertical walls appear, the embryo of *Asterella palmeri* undergoes transverse divisions which result in a filament of four cells. It seems likely that this develops by a transverse division of both hypobasal and epibasal segments of the fertilized egg.

11. It is suggested that the lowest cell of the young embryo gives rise to the foot, the next one to the seta, and the upper two to the capsule.

UNIVERSITY OF CALIFORNIA AT LOS ANGELES
CALIF.

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## LITERATURE CITED

1. ABRAMS, LE ROY, The structure and development of *Cryptomitrium tenerum*. BOT. GAZ. 28:110–121. 1899.
2. BARNES, C. R., and LAND, W. J. G., Bryological papers. I. The origin of air chambers. BOT. GAZ. 44:197–213. 1907.

3. CAMPBELL, D. H., The structure and development of mosses and ferns. 3d ed. New York. 1918.
4. DEUTSCH, H., A study of *Targionia hypophylla*. BOT. GAZ. **53**:492–503. 1912.
5. DUPLER, A. W., The air chambers of *Reboulia hemisphaerica*. Bull. Torr. Bot. Club **48**:241–252. 1921.
6. ——, The male receptacle and antheridium of *Reboulia hemisphaerica*. Amer. Jour. Bot. **9**:285–295. 1922.
7. ——, Early embryogeny of *Reboulia hemisphaerica*. BOT. GAZ. **74**:143–157. 1922.
8. EVANS, A. W., The air chambers of *Grimaldia fragrans*. Bull. Torr. Bot. Club **45**:235–251. 1918.
9. ——, The North American species of *Asterella*. Contrib. U.S. Nat. Herb. **20**:247–312. 1920.
10. GOEBEL, K., Organographie der Pflanzen. II. Spezielle Organographie. 2d ed. Jena. 1915.
11. HAUPT, A. W., Gametophyte and sex organs of *Reboulia hemisphaerica*. BOT. GAZ. **71**:61–74. 1921.
12. ——, Embryogeny and sporogenesis in *Reboulia hemisphaerica*. BOT. GAZ. **71**:446–453. 1921.
13. ——, Morphology of *Preissia quadrata*. BOT. GAZ. **82**:30–54. 1926.
14. HAYNES, C. C., HOWE, M. A., and EVANS, A. W., Sphaerocarpales-Marchantiales in *North American Flora*. **14**:1–66. 1923.
15. HOWE, M. A., The Hepaticae and Anthocerotes of California. Mem. Torr. Bot. Club **7**:1–208. 1899.
16. LEITGEB, H., Untersuchungen über die Lebermoose. VI. Die Marchantieen. Graz. 1881.
17. MEYER, K., Untersuchungen über den Sporophyt der Lebermoose. II. Die Entwickelungsgeschichte des Sporogons bei *Plagiochasma*. Bull. Soc. Imp. Nat. Moscow **27**:597–615. 1913.
18. ——, Über die Entwickelung des Sporogoniums bei *Preissia*. Moscow. 1915. (In Russian, with German summary.)
19. O'KEEFFE, LILLIAN, Structure and development of *Targionia hypophylla*. New Phytol. **14**:105–116. 1915.
20. PEISSEL, RUTH, Bau und Entwicklungsgeschichte von *Fimbriaria blumeana* Gottsche. Botan. Arch. **10**:434–476. 1925.
21. WOODBURN, W. L., Preliminary notes on the embryology of *Reboulia hemisphaerica*. Bull. Torr. Bot. Club **46**:461–464. 1920.

## EXPLANATION OF PLATE X

FIGS. 22–35.—Stages in development of antheridium; ×750.
FIG. 22.—Antheridium initial.
FIG. 23.—First division of same into basal and outer cells.

FIGS. 24–26.—Division of outer cell to form filament of four cells.

FIGS. 27–32.—Formation of vertical and additional transverse walls.

FIG. 33.—Completion of periclinal wall formation.

FIGS. 34, 35.—Unusual stages in early wall formation.

FIGS. 36–42.—Stages in development of archegonium; ×500.

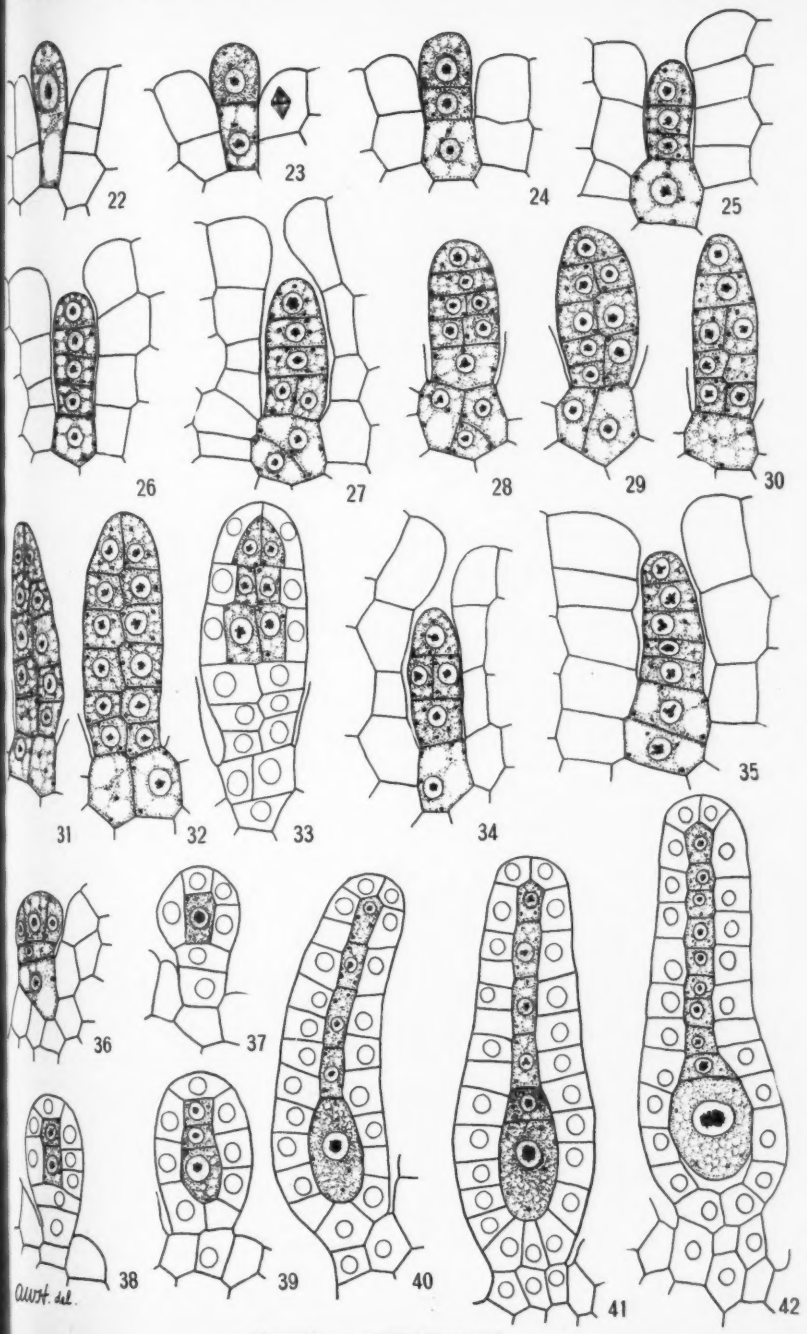
FIG. 36.—Formation of primary wall cells and division of basal cell.

FIG. 37.—Formation of cover cell and central cell from primary axial cell.

FIGS. 38–40.—Division of primary neck canal cell to form four neck canal cells, and formation of vertical wall in cover cell.

FIG. 41.—Differentiation of ventral canal cell and egg from primary ventral cell.

FIG. 42.—Mature archegonium showing increase in number of neck canal cells to eight.




HAUPT on HEPATICAE

# QUANTITATIVE DIFFERENCES IN PALISADE TISSUE IN CITRUS LEAVES[1]

F. F. HALMA

It was pointed out in a recent paper by HALMA and HAAS (2) that a greater percentage of the cross-sectional diameter of Eureka lemon leaves is occupied by palisade tissue than is found to be the case with Valencia orange leaves. Since these leaves came from only a few trees growing in the same locality, it was thought of importance to ascertain whether the quantitative difference in palisade tissue between these two citrus species is constant, and to include other species and varieties for comparison.

The data given herewith are believed to be extensive enough to warrant the conclusion that in healthy, fully mature leaves the ratio of the depth of the palisade tissue to the thickness of the leaf is nearly constant for each species.

All measurements were made on free-hand sections cut from the middle portion of the leaf. The values obtained for the depth of palisade tissue are expressed as a percentage of the leaf thickness. The following species and varieties were investigated: Eureka lemon, Lisbon lemon, Rough lemon, citron, Florida sour orange, Marsh seedless grapefruit, Dancy tangerine, Owari Satsuma, two hybrids (Rusk citrange and Sampson tangelo), and *Chalcas exotica* (a citrus relative).

In general arrangement of the leaf tissues these species resemble one another very closely. The majority of the leaves of Eureka and Lisbon lemon trees possess three rows of palisade cells, while as a rule the leaves of the other species and varieties possess only two rows. In many cases the third row is not continuous, hence was not included in the measurements. In nearly all cases there is, abutting against the palisade cells, a continuous row of round cells which were likewise excluded. No relation was found to exist between leaf thickness and palisade development. For example, Eureka lemon and Rough lemon leaves possess practically the same percentage of

[1] Paper no. 189, University of California, Graduate School of Tropical Agriculture and Citrus Experiment Station, Riverside, California.

palisade tissue, yet the average thickness of the latter is about 40μ less than that of the former. Moreover there is a wide range in leaf thickness within the species itself.

The leaf samples of Eureka lemon, Valencia orange, Navel orange, and grapefruit were obtained from young and old trees growing in the coastal and interior regions of southern California, while those of the remaining varieties were obtained only from the interior region.

It is apparent from table I that the values remain nearly constant for each species or variety, regardless of the age of the tree or its geographical distribution. *Chalcas exotica* ranks highest in palisade development, followed closely by the citron and the lemon group. The values then taper off gradually until we come to the Satsuma. The two hybrids are of interest in this connection. The Rusk citrange is a cross between the sweet orange and *Poncirus trifoliata*. The percentage of depth of palisade tissue of the leaves of the latter parent is about 32, but not enough leaves were examined before leaf fall to obtain a statistically reliable figure. Assuming that this number is approximately correct, it would mean that the degree of palisade development of leaves of the Rusk citrange occupies a place half way between that of its two parents. The tangelo, however, which is a cross between the tangerine and the grapefruit, ranks close to the grapefruit in palisade development (table I).

Since the palisade layers are considered to form the chief synthetic tissue, it is logical to assume that the species having leaves with highly developed palisade tissue should have a correspondingly high growth rate. It is a matter of common observation that seedlings of the lemon group grow much more rapidly than those of the orange group. Experiments with leafy cuttings of citrus (HALMA 3) show that rooting depends entirely on the presence of healthy, fully mature leaves. The rate at which the cuttings take root follows very closely the order of the degree of palisade development. Thus it is found that, in the order of rooting ability, *Chalcas exotica* stands at the head of the list, followed closely by citron, the lemon group, and Rusk citrange. The tangerines and oranges are much slower, the grapefruit still slower, and the Satsuma is the most difficult of all to root. Recent experiments with single leaf cuttings have given

TABLE I

DEPTH OF PALISADE TISSUE EXPRESSED AS PERCENTAGE OF LEAF THICKNESS

| VARIETY | SAMPLE | NO. OF LEAVES | MEAN | STANDARD DEVIATION |
|---|---|---|---|---|
| Chalcas exotica | 1 | 45 | 31.9±0.21 | 2.1±0.15 |
| Citron | 1 | 30 | 30.0±0.31 | 2.6±0.23 |
| Eureka lemon | 1 | 29 | 28.6±0.30 | 2.4±0.21 |
| | 2 | 32 | 28.7±0.20 | 1.7±0.14 |
| | 3 | 30 | 29.3±0.19 | 1.6±0.14 |
| | 4 | 30 | 29.4±0.23 | 1.9±0.16 |
| | 5 | 45 | 28.9±0.23 | 2.3±0.16 |
| | 6 | 28 | 28.3±0.20 | 1.6±0.14 |
| | 7 | 25 | 28.8±0.23 | 1.7±0.16 |
| | 8 | 30 | 29.2±0.14 | 1.2±0.10 |
| | 9 | 45 | 28.8±0.18 | 1.8±0.13 |
| | 10 | 30 | 29.2±0.16 | 1.3±0.11 |
| | 11 | 30 | 28.2±0.22 | 1.8±0.15 |
| | 1–11 | 354 | 28.8±0.07 | 2.0±0.05 |
| Lisbon lemon | 1 | 30 | 29.0±0.28 | 2.3±0.20 |
| Rough lemon | 1 | 30 | 28.2±0.23 | 1.9±0.16 |
| | 2 | 30 | 28.9±0.24 | 2.0±0.17 |
| Rusk citrange | 1 | 39 | 27.6±0.21 | 2.0±0.15 |
| Dancy tangerine | 1 | 30 | 25.0±0.29 | 2.4±0.21 |
| Sour orange | 1 | 26 | 24.3±0.23 | 1.8±0.16 |
| | 2 | 30 | 24.8±0.25 | 2.1±0.18 |
| Valencia orange | 1 | 33 | 23.9±0.28 | 2.4±0.20 |
| | 2 | 30 | 23.3±0.16 | 1.3±0.11 |
| | 3 | 37 | 24.7±0.25 | 2.3±0.18 |
| | 4 | 45 | 23.7±0.18 | 1.8±0.12 |
| | 5 | 30 | 23.3±0.30 | 2.5±0.21 |
| | 6 | 25 | 24.3±0.36 | 2.7±0.26 |
| | 7 | 30 | 24.3±0.29 | 2.4±0.21 |
| | 8 | 30 | 23.2±0.36 | 3.0±0.26 |
| | 9 | 30 | 23.7±0.34 | 2.8±0.24 |
| | 1–9 | 290 | 23.8±0.08 | 3.2±0.06 |
| Washington Navel orange | 1 | 39 | 23.3±0.25 | 2.3±0.17 |
| | 2 | 30 | 22.8±0.19 | 1.6±0.14 |
| | 3 | 30 | 22.4±0.25 | 2.1±0.18 |
| | 4 | 30 | 22.6±0.18 | 1.5±0.13 |
| | 1–4 | 129 | 22.8±0.12 | 2.0±0.08 |
| Marsh grapefruit | 1 | 30 | 22.0±0.18 | 1.5±0.13 |
| | 2 | 30 | 21.6±0.21 | 1.7±0.15 |
| | 3 | 30 | 22.3±0.26 | 2.2±0.19 |
| | 4 | 33 | 21.6±0.19 | 1.6±0.13 |
| | 5 | 33 | 22.0±0.26 | 2.3±0.19 |
| | 6 | 30 | 20.7±0.24 | 2.0±0.17 |
| | 7 | 30 | 21.3±0.26 | 2.2±0.19 |
| | 1–7 | 216 | 21.6±0.09 | 2.1±0.06 |
| Sampson tangelo | 1 | 30 | 21.6±0.25 | 2.1±0.18 |
| Owari Satsuma | 1 | 32 | 21.2±0.20 | 1.7±0.14 |
| | 2 | 30 | 20.9±0.19 | 1.6±0.14 |

similar results. There is the possibility, however, that the leaves of those species which root most rapidly contain more stored carbohydrates than leaves of slow-rooting species. This point needs to be investigated. Unpublished observations show that when rooted cuttings having a similar leaf area are planted in the nursery, the rate of subsequent growth follows the same general order as given for the palisade development (table I). In this connection it is of interest to mention the recent work of ALEXANDROV (1), who found that the ratio of depth of palisade tissue to thickness of leaf differed in the three varieties of grapes which he investigated. He speculates that these findings may be of great practical importance, since the variety

TABLE II

DEPTH OF PALISADE TISSUE; HEAVILY SHADED "ABNORMAL" INTERIOR LEAVES COMPARED WITH NORMAL LEAVES (30 IN EACH SAMPLE)

| | NORMAL | | ABNORMAL | |
|---|---|---|---|---|
| | Mean | Standard deviation | Mean | Standard deviation |
| Eureka lemon..... | 28.6±0.22 | 1.8±0.15 | 21.9±0.22 | 1.8±0.15 |
| Valencia orange..... | 23.7±0.22 | 1.8±0.15 | 19.6±0.25 | 2.1±0.18 |
| Marsh grapefruit.... | 21.6±0.19 | 1.6±0.14 | 19.1±0.28 | 2.3±0.20 |

having the greatest number of palisade cells is the most productive and the one with the least number the least productive.

There are numerous references regarding the influence of environmental factors upon palisade development. For example, LANGNER (4) reports that the palisade tissue is two to three times as thick in a sun leaf as in a shade leaf of *Acer pseudoplatanus*. Citrus leaves collected from the north and south sides of the tree failed to reveal any differences in degree of palisade development; likewise no difference was found between leaves taken from the upper and lower parts of the tree. However, leaves taken from devitalized branches of the dense interior portion showed a marked decrease in the percentage of palisade tissue as compared with the general average. Although mature, these leaves are thin and in many respects appear subnormal. An interesting point observed with this type of leaf is that the lemon leaf still possesses a greater percentage of palisade

tissue than the Valencia, and that the latter exceeds the grapefruit, as is shown in table II.

The effect of soil moisture was not investigated. A possible influence of rootstock on palisade development was considered. Samples of leaves were obtained from Eureka lemon and Valencia orange trees growing on rootstocks of sweet orange, sour orange, grapefruit, and *Poncirus trifoliata*. In addition, leaves were obtained from three different old lemon trees growing on their own roots. The results were the same as those given in table I.

The quantitative difference in palisade development in leaves of different ages was ascertained in the Eureka lemon and is shown in

TABLE III

DEPTH OF PALISADE TISSUE (30 LEAVES IN EACH SAMPLE); CHANGE WITH AGE OF LEAF (EUREKA LEMON)

| APPROXIMATE AGE (MONTHS) | CONDITION | MEAN | STANDARD DEVIATION |
|---|---|---|---|
| 12 | Full mature | 29.2±0.16 | 1.3±0.11 |
| 8 | Full mature | 28.2±0.22 | 1.8±0.15 |
| 5 | Full-sized, but thin | 26.6±0.16 | 1.3±0.11 |
| 2 | Full-sized, light green | 23.7±0.30 | 2.5±0.21 |

table III. It will be noted that the two-months-old lemon leaves, which are still immature, average as high as fully mature leaves of the Valencia orange (table I). It is of interest in this connection that cuttings having immature leaves do not root readily. In conclusion it may be mentioned that the quantitative relationship between palisade development and root production of citrus is being investigated.

## Summary

1. The ratio of depth of palisade tissue to leaf thickness was found to be nearly constant for each species or variety of citrus examined.

2. Leaves of the lemon group show a value which is approximately 20 per cent higher than that for leaves of the orange. The grapefruit ranks below the orange, and the Satsuma shows the lowest value.

3. The close relationship which exists between the degree of palisade development for each species and its growth rate is discussed.

UNIVERSITY OF CALIFORNIA
CITRUS EXPERIMENT STATION
RIVERSIDE, CALIF.

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## LITERATURE CITED

1. ALEXANDROV, W. G., Versuch einer quantitativ-anatomischen Charakteristik der Grundsorten von Weinreben Kachetiens. Ber. Deutsch. Bot. Ges. 45: 429–436. 1927.
2. HALMA, F. F., and HAAS, A. R. C., Effect of sunlight on sap concentration of citrus leaves. BOT. GAZ. 86: 102–106. 1928.
3. HALMA, F. F., Propagating citrus by cuttings. Calif. Citrograph 11: 225. 1926.
4. LANGNER, W., Über die Verteilung der Stärke in Laubblättern zu verschiedenen Tageszeiten. Jahrb. Wiss. Bot. 67: 291–333. 1927.

# CURRENT LITERATURE

## BOOK REVIEWS

### Creation by evolution

Probably sufficient popular interest in evolution remains to insure the success of the latest collaborative volume[1] on the subject. This book, under the editorship of FRANCES MASON, is surely authoritative and readable; parts of it are thrilling.

A foreword is provided by HENRY FAIRFIELD OSBORN (Columbia), and an introduction by Sir C. S. SHERRINGTON (Oxford). DAVID STARR JORDAN (Leland Stanford), building upon the isolation which he himself has made famous, concludes that evolution is merely another name for nature. J. ARTHUR THOMSON (Aberdeen) argues that the cumulative effect of the many different lines of evidence forces us to accept evolution; then furnishes the faint-hearted with the following encouragement: "There are great trends discernible in organic evolution, and the greatest of these are toward health and beauty; toward the love of mates, parental care, and family affection; toward clear-headedness and healthy-mindedness; and the momentum of these trends is with us at our best."

H. S. JENNINGS (Johns Hopkins) very simply demonstrates by his own experiments on protozoa that we can actually see evolution occurring among simpler animals.

Following G. H. PARKER's (Harvard) cases of vestigial organs, E. W. MACBRIDE (London) and E. G. CONKLIN (Princeton) divide the task of outlining the embryological evidence for evolution. The former apparently weakens his argument for the sophisticated reader by utilizing inheritance of acquired characters. CONKLIN effectively points his discussion with the following thought: "Religious faith has been able to survive the knowledge of the fact that every human being in the world has come into existence by a process of development. Why should it be supposed that the recognition of an equally natural development of groups of individuals or species would be destructive of religion?"

W. B. SCOTT (Princeton) very temperately undertakes to "support the hypothesis of evolution" with the known facts of present and recent geographical distribution of animals, and more than succeeds. His story of the mammals of the Americas will interest the reader in much the same way as does a historical novel. In the simplest terms, F. A. BATHER (British Museum) explains the validity of fossil evidence.

J. W. GREGORY (Glasgow) gives reasons for abandoning the unnatural and

[1] Creation by evolution, edited by FRANCES MASON. 8vo. pp. xx+392. New York: Macmillan Co. 1928. $5.00.

anti-evolutionary term "species." As a substitute he recommends his own term "circulus," "a natural grouping which has a center of organic stability, and most of its members tend to be near the center so long as the conditions remain the same."

The evolution of animal and plant kingdoms is sketched by Sir ARTHUR SMITH WOODWARD (British Museum) and C. S. GAGER (Brooklyn) respectively. E. W. BERRY (Johns Hopkins) follows with the story as told by fossil plants.

Several special groups of animals are treated in the following chapters. E. B. POULTON (Oxford) has an excellent chapter on butterflies. Surely one must agree that a study of the habits, development, and recent history of this group alone is enough to convince the student of the truth of evolution. Sir A. E. SHIPLEY (Cambridge) follows the evolutionary steps among bees from primitive types to the bumble bee, with its almost human society, and beyond to the honey bee, with its decidedly super-human social organization. W. M. WHEELER (Harvard) tells of the still more remarkable ants, whose evolution had already carried them to a state of social perfection millions of years ago. F. B. LOOMIS (Amherst) gives an animated outline of the fossil records of the horse and elephant. In business-like style, D. M. S. WATSON (London) sketches the evolution of the bird from the lizard ancestor, through the dinosaur-like stage, to *Archaeopteryx*, the toothed fossil bird which was no more efficient at flying than the modern aeroplane, culminating in the bird of the present, which provides a model for the aeroplane of the future.

R. S. LULL (Yale) and W. J. GREGORY (Columbia) divide the task of describing what we know of man's own direct ancestry, and explain why we do not as yet know more. S. K. HOLMES (California) shows us that our simian cousins are more human than we had suspected.

J. S. HUXLEY'S (London) evaluation of evolutionary progress is excellent. C. L. MORGAN'S (Bristol) vague chapter on "mind in evolution" will prove more useful to the preacher than to the lay reader. In the concluding chapter, H. H. NEWMAN (Chicago) illustrates how the numerous separate lines of evidence for evolution are corroborative, not only in principle but in detail.

Just why no chapter on experimental evolution among higher organisms was included is puzzling to the reviewer. Perhaps the volume was designed to reveal merely what evolution has accomplished, rather than to analyze how the process is carried out.—M. C. COULTER.

### Ecological evolution of angiosperms

One of the most stimulating books that has come recently to hand is by BEWS,[2] well known to all ecologists for his studies of South African vegetation. In the present volume the author attempts to apply the facts and theories of ecology to the problems involved in angiosperm evolution. The whole work is

[2] BEWS, J. W., Studies in the ecological evolution of the angiosperms. 8vo. pp. viii +134. London: Wheldon & Wesley, Ltd. 1927. 8*s*.

strongly colored, and naturally so, by BEWS' long African experience. He sees angiosperm evolution largely from the tropical viewpoint, and states that to look at the subject from the viewpoint of the north temperate zone is to glimpse through the wrong end of the telescope. It was in the warmer climates that angiosperms doubtless had their beginnings, and it is in the warmer climates of our present world that we may expect to find the most representative of primitive angiosperms. In Cretaceous times and through much of the Tertiary the climates of the world were largely similar, and moist; but in more recent times have come climatic differentiations in the extratropical regions. It is in these regions that most recent evolution has probably taken place. The author shows that in most of the families and orders of the dicotyledons the tropical forms are more primitive and arboreal, whereas in the temperate zones we have the more recent and herbaceous forms. On the whole the fossil evidence fits in with this idea, although of course there are all too many imperfections in the record. The author discusses with much interesting detail the anatomical and other characteristics of the primitive tropical trees, in contrast with the characteristics of the more advanced types of colder or drier regions. He traces the supposed evolution of lianas from tropical trees, and of epiphytes from lianas. Water plants and annuals are regarded as relatively late products of evolution. Very interesting is his discussion of the Ericaceae. Usually the northern forms in this family are regarded as the main group, and the South African forms are thought to be detached outliers. BEWS thinks, however, that the South African Ericaceae are the more primitive, for they are much more numerous as to species, and in other respects reveal that they are older.

All ecologists should read and digest this interesting volume by BEWS; while it is speculative and at times quite unorthodox, it is suggestive and refreshing.—H. C. COWLES.

### Textbook of general botany

A revised edition of the textbook by SMITH, OVERTON, GILBERT, DENNISTON, BRYAN, and ALLEN has just been published.[3] The new volume is a revision and enlargement of the first, which was published in 1926. It contains 130 additional pages and nearly 100 new figures. The chapters on roots, stems, leaves, and relations of plants to water have been expanded and many excellent figures added. The treatment of the Thallophytes is one of the noteworthy changes which improve the new edition. In this section the algae are adequately treated; new forms are included in the chapter on green algae; and new chapters have been introduced on the brown and red algae which were discussed very briefly in the first edition. In its present form the book represents a well organized survey of the field in general botany, and should serve as an excellent

[3] SMITH, G. M., OVERTON, J. B., GILBERT, E. M., DENNISTON, H. H., BRYAN, G. S., ALLEN, C. E., A textbook of general botany. 8vo. x+539. *figs. 416*. New York: MacMillan Co. 1928.

book of reference. It is so arranged that, by selecting to meet individual needs, the book can be used for a semester course in elementary botany.—H. E. HAYWARD.

## NOTES FOR STUDENTS

**Taxonomic notes.**—COKER[4] has published an account of 15 species of Basidiomycetes, 3 of which are described as new. He also has published a full account of the 8 Chapel Hill species of *Psalliota*.

PENNELL[5] has described a new *Scrophularia* (*S. oregana*) from Oregon, and a new *Pedicularis* (*P. rainierensis*) from Washington.

PECK[6] has described new species of *Calochortus*, *Ribes*, *Hydrophyllum*, *Veronica*, and *Hieracium* from Oregon, and also new varieties in other genera.

BROWN[7] has described a new genus (*Bijlia*) of Mesembryaceae from South Africa. It is based upon a recent specimen which proves to represent a "long lost" species described under another name.

NADSON and KRASSILNIKOV[8] have described a new genus (*Guilliermondella*) of Endomycetes found in Kalouga, Russia. The description is based on numerous cultures under various conditions.

THÉRIOT[9] has published the second part of his account of the mosses collected by BROUARD in Mexico, the first part having been published in 1926. He announces that the third part is in preparation. The present part includes 102 species, in 40 genera. The large genera are *Bryum* (14 spp.) and *Brachymenium* (12 spp.). Only 6 species are described as new.—J. M. C.

**The middle lamella.**—For many years it has been believed by plant physiologists that the middle lamella between plant cells consists of calcium pectate. Three years ago RITTER[10] brought forward evidence that at least in woody tissues it was not even pectic in nature, but consisted of lignin. HARLOW[11] has recently confirmed this work, but has shown that in all parenchymatous tissues

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[4] COKER, W. C., Notes on Basidiomycetes and the Chapel Hill species of the genus *Psalliota*. Jour. Elisha Mitchell Sci. Soc. **43**:233–256. 1928.

[5] PENNELL, F. W., Notes on Scrophulariaceae of the northwestern United States. Bull. Torr. Bot. Club **55**:315–318. 1928.

[6] PECK, M. E., New plants from Oregon. Torreya **28**:53–57. 1928.

[7] BROWN, N. E., *Mesembryanthemum* and allied genera. Jour. Bot. **66**:265–268. 1928.

[8] NADSON, G., and KRASSILNIKOV, N., Un nouveau genre d' Endomycétacées: *Guilliermondella*. Comptes Rendus Acad. Sci., **187**:307–309. 1928.

[9] THÉRIOT, I., Mexican mosses collected by Brother Arsène Brouard. II. Smithsonian Miscell. Coll. **81**:1–26. 1928.

[10] RITTER, G. J., The distribution of lignin in wood. Jour. Ind. Eng. Chem. **17**: 1194–1195. 1925.

[11] HARLOW, W. M., The chemical nature of the middle lamella. N.Y. State Col. For. (Syracuse) Tech. Publ. **21**:1–11. 1927.

it is of pectic substance, as MANGIN first stated. Both these recent workers have relied on solubility tests and not simply on staining reactions, and have shown that our supposedly reliable Ruthenium red is not as reliable a pectic stain as has been supposed.

It may be, however, that we shall have to abandon the view long held that the middle lamella is calcium pectate, although insufficient evidence has been accumulated to prove this point. But the chemists have recently legislated that the middle lamella is protopectin, that is, the pectose of plant physiologists and plant chemists for nearly a century now. In the report of the Committee on Nomenclature of Pectin of the Agriculture-Food Division of the American Chemical Society,[12] the enzyme protopectinase is defined as "the enzyme which hydrolyzes or dissolves protopectin with the resultant separation of plant cells from each other," thus specifically defining the middle lamella as consisting of protopectin. Presumably the evidence considered as justifying this step is the finding that cold alkali oxalates do not dissolve the middle lamella although they dissolve pectates. This is reported, for instance, by CONRAD[13] and by DAVISON and WILLAMAN[14] recently. On the other hand, plant microchemists have long used dilute acid followed by dilute alkali to dissolve the middle lamella, and this is a treatment of which protopectin should need only the first step.

It will be worth while to abandon the old and established term "pectose" in favor of "protopectin," if thereby we may obtain uniformity of nomenclature; but plant physiologists will regret having the chemical nature of the middle lamella settled for them by legislation rather than by experimentation.—H. S. WOLFE.

**North American Flora.**—The second part of volume 23 continues the presentation of the Mimosaceae by N. L. BRITTON and J. N. ROSE. The tribe Ingeae is concluded by the presentation of *Lysiloma*, with 31 species, 20 of which are new. The next tribe, Acacieae, includes 12 genera, 8 of which are separated from *Acacia* as new genera, leaving that genus represented by one species. The new genera are *Tauroceras* (2 species), *Bahamia* (1 species), *Feracacia* (2 species), *Lucaya* (1 species), *Fishlockia* (1 species), *Myrmecodendron* (11 species, one being new), *Acaciopsis* (14 species, one being new), and *Acaciella* (49 species, 26 being new). *Senegalia* includes 66 species, 27 being new. The third tribe, Mimoseae, includes 12 genera, 4 of which are presented. They are *Leucaena* (39 species, 22 new) and *Acuan* (26 species, 13 new), and the new genera *Ryncholeucaena* and *Caudoleucaena*, each with a single species.—J. M. C.

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[12] Jour. Amer. Chem. Soc. 49. Proc. 37–39. 1927. See also the same report quoted in footnote 14.

[13] CONRAD, C. M., A biochemical study of insoluble pectic substances in vegetables. Amer. Jour. Bot. 13:531–547. 1926.

[14] DAVISON, F. R., and WILLAMAN, J. J., Pectic enzymes. BOT. GAZ. 83:329–362. 1927.

**Boron and plant growth.**—Recent work has added at least three elements to the original list of ten which research had shown were needed for the growth of plants. These are boron, zinc, and manganese. Of these three elements, perhaps boron has received most attention, at least in recent investigation. The work of such English investigators as WARINGTON, BRENCHLEY, and others, has shown a possible function of boron, by indicating a connection between it and the absorption and utilization of calcium by the plant. Also the work has shown that boron is needed for proper plant development, and to prevent the disintegration of the vascular elements.

JOHNSTON and DORE[15] have recently secured results that are in agreement with these anatomical studies. It was found that the leaves of tomato plants, grown in boron-deficient solutions, had more starch and about twice as much total sugar as plants grown in solutions containing boron; on the other hand, the stems of the boron-deficient plants contained only about two-thirds as much sugar as the normal plants. When boron was lacking in the nutrient solution the plants developed a purple color which was probably due to anthocyanin. It is well known that this pigment often develops to a greater extent in tissue containing a large amount of sugar. Examination by PRIESTLEY of the petioles and stems showed that in the case of the boron-deficient plants the phloem had disintegrated, and seemed to have a decidedly more acid reaction than the phloem of normal plants; so the accumulation of carbohydrates in the leaves would seem to be due to a breakdown of the conductive system. Other characteristics of the boron-deficient plants are noted.—S. V. EATON.

**Forest trees of Hokkaido, Japan.**—The forests of Japan must be beautiful indeed if their elements are accurately represented in the fine colored plates that comprise the fascicles by MIYABE and KUDO.[16] It is also very convenient to have the descriptions of the various species in English as well as in Japanese. More than a dozen fascicles have already been noted in this journal,[17] and the five now appearing include plates and descriptions of *Magnolia obovata*, *M. kobus*, *Hydrangea paniculata*, *Malus baccata* var. *mandshurica*, *Sorbus commixa*, *Micromeles alnifolia*, *Photinia villosa*, *Crataegus jozana*, *Prunus maximowiczii*, *P. sargentii*, *P. kurilensis*, *P. padus*, *P. grayana*, *P. ssiori*, and *Maackia amurensis* var. *buergeri*.—G. D. FULLER.

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[15] JOHNSTON, E. S., and DORE, W. H., The relation of boron to the growth of plants. Science **67**:324–325. 1928.

[16] MIYABE, K., and KUDO, Y., Icones of the essential forest trees of Hokkaido. Publ. by Hokkaido Government, Sapporo **2**: Fasc. 15. 27–32. *pls. 44–46*. 1927; Fasc. 16. 33–38. *pls. 50–52*. 1927; Fasc. 17. 39–44. *pls. 50–52*. 1927; Fasc. 18. 45–52. *pls. 53–55*. 1927; Fasc. 19. 53–58. *pls. 56–58*. 1928.

[17] BOT. GAZ. **72**:55. 1921; **75**:431. 1923; **83**:328. 1927.